FIRM/R 291

FAO Fisheries Report No. 291, Volume 3
FAO, Informe de Pesca N° 291, Volumen 3
FIRM/R291 Vol. 3

PROCEEDINGS OF THE EXPERT CONSULTATION TO EXAMINE CHANGES IN ABUNDANCE AND SPECIES COMPOSITION OF NERITIC FISH RESOURCES

San José, Costa Rica, 18-29 April 1983

ACTAS DE LA CONSULTA DE EXPERTOS PARA EXAMINAR LOS CAMBIOS EN LA ABUNDANCIA Y COMPOSICION POR ESPECIES DE RECURSOS DE PECES NERITICOS

San José, Costa Rica, 18-29 de abril de 1983

LIBRARY
JUN [illegible] 1984
National [illegible] Service
2570 Dole Street
Honolulu, Hawaii

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ORGANIZACION DE LAS NACIONES UNIDAS PARA LA AGRICULTURA Y LA ALIMENTACION

Digitized by the Internet Archive
in 2025

https://archive.org/details/fao-fisheries-and-aquaculture-report_1983_3_291

FAO Fisheries Report No. 291, Volume 3
FAO, Informes de Pesca, N° 291, Volumen 3 FIRM/R291 Vol.3(En/Es)

PROCEEDINGS OF THE EXPERT CONSULTATION TO EXAMINE CHANGES IN ABUNDANCE AND SPECIES COMPOSITION OF NERITIC FISH RESOURCES

SAN JOSE, COSTA RICA
18-29 APRIL 1983

ACTAS DE LA CONSULTA DE EXPERTOS PARA EXAMINAR LOS CAMBIOS EN LA ABUNDANCIA Y COMPOSICION POR ESPECIES DE RECURSOS DE PECES NERITICOS

SAN JOSE, COSTA RICA
18-29 ABRIL 1983

Edited by
Editadas por

G.D. Sharp and/y J. Csirke
Fisheries Department/Departamento de Pesca

A preparatory meeting for the FAO World Conference on Fisheries Management and Development

Una reunión preparatoria para la Conferencia Mundial de la FAO sobre Ordenación y Desarrollo Pesqueros

Food and Agriculture Organization of the United Nations
Organización de las Naciones Unidas para la Agricultura y la Alimentación
Rome/Roma 1983

FAO FISHERIES REPORT No. 291, VOLUME 3

CORRIGENDUM: On the reverse of the title page, the ISBN (job identification) number should appear as ISBN 92-5-001447-3 (not 101447).

© FAO 1983

PREPARATION OF THIS DOCUMENT

These proceedings consist of the papers that were presented and discussed during the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources held in San José, Costa Rica, 18-29 April 1983. The Reports of the Expert Consultation are published in Volume 1 of this FAO Fisheries Report No. 291. The first part of the Proceedings is published in Volume 2 of this Fisheries Report which contains all the papers giving regional reviews describing environmental and resources changes and related fisheries responses.

This volume contains Parts 2, 3 and 4 of the Proceedings with papers dealing respectively with localized and comparative studies, impacts of environmental and resources variability on human communities, and application of methods and theory. All papers are published in the original language in which they were presented to the Consultation, either in English or Spanish, with a summary in the other language.

This document was reviewed and edited by Drs. J. Csirke and G.D. Sharp, Technical Secretaries of the Expert Consultation, Mrs. Yvette Corsetti and Miss Graciela Segura were responsible for the bulk of the typing and preparation of this volume, aided at different times by Doris Dearing, Sally Den Hertog-Riccardi, Jacqueline Ellis, Suzanne Tyrrell-Donati, Jean Valletta, Janet Webb-Savini. Ms. Kathleen T. Dorsey assisted with the proof-reading and Drs. S. Garcia and S. Chikuni helped with the review of some of the papers.

This Expert Consultation was one of the preparatory meetings for the FAO World Conference on Fisheries Management and Development. The Consultation was organized by FAO, with the support of IOC, CPPS, DANIDA, ICLARM, ICSEAF, IDB, SELA and WMO.

PREPARACION DE ESTE DOCUMENTO

Estas actas contienen las contribuciones que fueron presentadas y discutidas durante la Consulta de Expertos para Examinar los Cambios en la Abundancia y Composición por Especies de Recursos de Peces Nerfticos que se realizó en San José, Costa Rica, del 18 al 29 de Abril de 1983. Los Informes de la Consulta de Expertos están publicados en el Volumen 1 de este FAO, Informes de Pesca No. 291. La primera parte de estas actas están publicadas en el volumen 2 de este Informe de Pesca y contiene las contribuciones donde se hacen revisiones regionales de los cambios en el medio ambiente y en los recursos y de las reacciones correspondientes en el campo de la pesca.

Este volumen contiene las partes 2, 3 y 4 de las actas, con las contribuciones que tratan respectivamente sobre estudios lozalizados y comparativos, sobre las repercusiones de la variabilidad del ambiente y de los recursos en las comunidades humanas, y sobre la aplicación de métodos y teorfa. Todas las contribuciones se han publicado en el idioma original en que fueron presentadas a la Consulta de Expertos, ya sea en español o inglés, con un resumen en el otro idioma.

Este documento ha sido revisado y editado por los Drs. J. Csirke y G.D. Sharp, los dos Secretarios Técnicos de la Consulta de Expertos. La Sra. Yvette Corsetti y la Srta. Graciela Segura fueron responsables de la mayor parte del trabajo de mecanografiado y preparación de este volumen, con la asistencia temporal de Doris Dearing, Sally Den Hertog-Riccardi, Jacqueline Ellis, Suzanne Tyrrell-Donati, Jean Valletta, Janet Webb-Savini. La Sra. Kathleen T. Dorsey asistió en la corrección de las pruebas y los Drs. S. Garcia y S. Chikuni asistieron con la revisión de algunos de los documentos.

Esta Consulta de Expertos fue una de las reuniones preparatorias para la Conferencia Mundial de la FAO sobre Ordenación y Desarrollo Pesqueros. La consulta fue organizada por la FAO con el apoyo de la COI, BID, CIPASO, CPPS, DANIDA, ICLARM, OMM y SELA.

Distribution/Distribución:

FAO Fisheries Department
FAO Regional Fisheries Officers
Directors of Fisheries
Selector SM
Participants

Departamento de Pesca de la FAO
Oficiales Regionales de Pesca
de la FAO
Directores de Pesca
Selector SM
Participantes

For bibliographic purposes this document should be cited as follows/Para fines bibliográficas, este documento debe ser citado como sigue:

Sharp, G.D. and/y J. Csirke (eds), Proceedings
1983 of the Expert Consultation to examine changes in abundance and species of neritic fish resources. San José, Costa, Rica, 18-29 April 1983. Actas de la Consulta de Expertos para examinar los cambios en la abundancia y composición por especies de recursos de peces neríticos. San José, Costa Rica, 18-29 abril 1983. A preparatory meeting for the FAO World Conference on fisheries management and development. Una reunión preparatoria para la Conferencia Mundial de la FAO sobre ordenación y desarrollo pesqueros. FAO Fish.Rep./FAO, Inf.Pesca, (291) Vol.3:557-1224

TABLE OF CONTENTS
TABLA DE CONTENIDO

Pag.

PART II.- LOCALIZED AND COMPARATIVE STUDIES
PARTE II.- ESTUDIOS LOCALIZADOS Y COMPARATIVOS

Ocean scale and regional comparison - Estudios oceánicos y comparación regional

Influence of the ocean on the atmospheric global circulations and short-range climatic fluctuations, by *T. Tokioka* 557

El rol de la temperatura superficial del mar y la subsidencia atmosférica en la descripción de la estructura térmica de la capa de inversión, por *P. Lagos* 587

Climatic change: past lessons and future prospects, by *P.M. Kelly* 595

Condiciones oceanográficas y sus fluctuaciones en el Pacífico sur oriental, por *O. Guillén* 607

Physics and fish populations: shelf sea fronts and fisheries, by *J. Hunter* and *G.D. Sharp* 659

Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú, por *P.A. Bernal* *F.L. Robles* y *O. Rojas* 683

Variabilidad biológica de baja frecuencia y gran escala en la corriente de California 1949-1978, por *P.A. Bernal* y *D.B. Chelton* 713

Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, by *R.A. Parrish* *A. Bakun* *D.M. Husby* and *C.S. Nelson* 731

Local studies - Estudios locales

Species interactions in the dynamics of planktivorous fish assemblages in Lake Michigan, by *J.J. Magnuson* and *L.B. Crowder* 779

Population dynamics and factors affecting the abundance of capelin (*Mallotus villosus*) in the northwest Atlantic, by *J.E. Carscadden* 789

Herring and sprat: fishery independent variations in abundance, by *A. Lindquist* 813

Monsoon-induced seasonality in the recruitment of Philippine fishes, by *D. Pauly* and *N.A. Navaluna* 823

Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del ambiente marino frente al Perú, por *H. Santander* y *R. Flores* 835

PART III.- IMPACTS OF ENVIRONMENTAL AND RESOURCES VARIABILITY ON HUMAN COMMUNITIES
PARTE III.- REPERCUSIONES DE LA VARIABILIDAD DEL AMBIENTE Y DE LOS RECURSOS EN LAS COMUNIDADES HUMANAS

Man, state and fisheries: an inquiry into some societal constraints that affect fisheries management, by *M. H. Glantz* 871

Science and decision-making in fisheries regulation, by *R.J.H. Beverton* 919

Pag.

PART IV.- APPLICATION OF METHODS AND THEORY
PARTE IV.- APLICATION DE METODOS Y TEORIA

Vertical distribution of larvae of mackerel (*Scomber scombrus*) and microplankton, with some conclusions on feeding conditions and survey methods, by *S. H. Coombs*, *J.A. Lindley* and *C.A. Fosh* 939

Fluctuaciones de poblaciones de aves guaneras en el litoral peruano, 1960-1981, por *H. Tovar* 957

Batch fecundity and spawning frequency of various anchovy (Genus: *Engraulis*) populations from upwelling areas and their use for spawning biomass estimates, by *J. Alheit*, *B. Alegre*, *V.H. Alarcón* and *B. Macewicz* 977

On the seasonal growth, monthly recruitment and monthly biomass of Peruvian anchoveta (*Engraulis ringens*) from 1961 to 1979, by *D. Pauly* and *I. Tsukayama* 987

Body length variability in fish schools and cohorts; application to fisheries biology in tropical waters, by *P. Fréon* 1005

Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*), by *H. Santander*, *J. Alheit*, *A.D. MacCall* and *A. Alamo* 1011

Comparison of egg sample probability distributions of the anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) off Peru and the anchovy (*E. mordax*) and the sardine (*Sardinops caerulea*) off California, by *P.E. Smith*, *H. Santander* and *J. Alheit* 1027

On the variability of population biology rates: examples from the California pelagic fisheries (Summary only), by *R.H. Parrish* and *D.L. Mallicoate* 1039

On long term changes in abiotic and biotic conditions, by *A.A. Elizarov* 1041

Estudio comparativo de la dinámica de una especie pelágica y otra demersal mediante un modelo de simulación (sólo resumen), por *J. Lleonart* y *B. Roel* 1045

Production models as applied to sub-stocks depending on upwelling fluctuations, by *P. Fréon* 1047

Why do some pelagic fishes have wide fluctuations in their numbers? - Biological basis of fluctuation from the viewpoint of evolutionary ecology, by *T. Kawasaki* 1065

Change in abundance and species composition of neritic pelagic fish stocks in connection with larval mortality caused by cannibalism and predatory loss by carnivorous plankton, by *T. Kawai* and *K. Isibasi* 1081

Variations in the parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system, by *P.A. Shelton* and *M.J. Armstrong* 1113

Interactions of pelagic fishes and the relation between environmental factors and abundance, by *B.E. Skud* 1133

Managing variable fishery stocks in an uncertain environment - the design of fishery management systems, by *B.J. Rothschild* and *D.G. Heimbuch* 1141

Applications of a Laevastu-Larkins ecosystem model for Bering Sea groundfish management, by *Loh-Lee Low* 1161

Modelling fisheries: what was the question?, by *G.D. Sharp*, *J. Csirke* and *S. García* 1177

PART II - LOCALIZED AND COMPARATIVE STUDIES

PARTE II - ESTUDIOS LOCALIZADOS Y COMPARATIVOS

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

INFLUENCE OF THE OCEAN ON THE ATMOSPHERIC GLOBAL CIRCULATIONS AND SHORT-RANGE CLIMATIC FLUCTUATIONS

by

Tatsushi Tokioka

Meteorological Research Institute
Nagamine 1-1, Tsukuba, Ibaraki 305
Japan

Resumen

Alrededor del 70% de la superficie de la tierra está cubierta por los océanos. Se reconoce que los intercambios de energía y momentum entre la atmósfera y el océano son muy importantes para mantener la circulación global de la atmósfera. Otro aspecto importante del océano es su amplia inercia térmica comparada con la de la atmósfera y la superficie de la tierra. La anomalía térmica observada en la parte superior del océano tiene un tiempo de persistencia de varios meses lo que es casi un orden de magnitud mayor que las anomalías dentro de la atmósfera. Por esta razón, se considera que la anomalía de la temperatura de la superficie del mar es uno de los frentes superficiales más importantes para los fines de predicción de corto alcance de las fluctuaciones climáticas.

Han habido estudios muy activos donde se han descubierto relaciones entre las anomalías de la temperatura de la superficie del mar y la circulación anómala dentro de la atmósfera. Una de las variaciones no estacionales más notables observadas en la temperatura superficial del mar es aquella asociada con el fenómeno de El Niño. En la etapa madura de El Niño, la mitad oriental del océano Pacífico tropical tiene una temperatura superficial del mar que es mucho más cálida de lo normal. Al mismo tiempo la parte occidental del océano Pacífico subtropical está cubierto de una temperatura superficial del mar más fría que lo normal.

Durante el fenómeno de El Niño se observan fuertes lluvias en el área de anomalía cálida de la temperatura de la superficie del mar. Se presenta una liberación anómala del calor latente en la misma región, lo que causa cambios en las circulaciones este-oeste (circulación de Walker) en su ubicación e intensidad dentro de los trópicos. En las bajas latitudes también se observa una marcada anomalía de número de onda 1 en dirección este-oeste en la presión a nivel del mar. Esto coincide con el fenómeno que por mucho tiempo ha sido reconocido como Oscilación del Sur. Independientemente de la longitud, en la parte superior de la tropósfera tropical se observan temperaturas más altas y una mayor altura geopotencial.

En base a las observaciones se ha establecido que durante el fenómeno de El Niño las anomalías de la circulación de la atmósfera se extienden hacia latitudes extratropicales en el invierno del hemisferio norte. El mecanismo de teleconección puede ser explicado como una propagación de las ondas externas de Rossby dentro de la atmósfera.

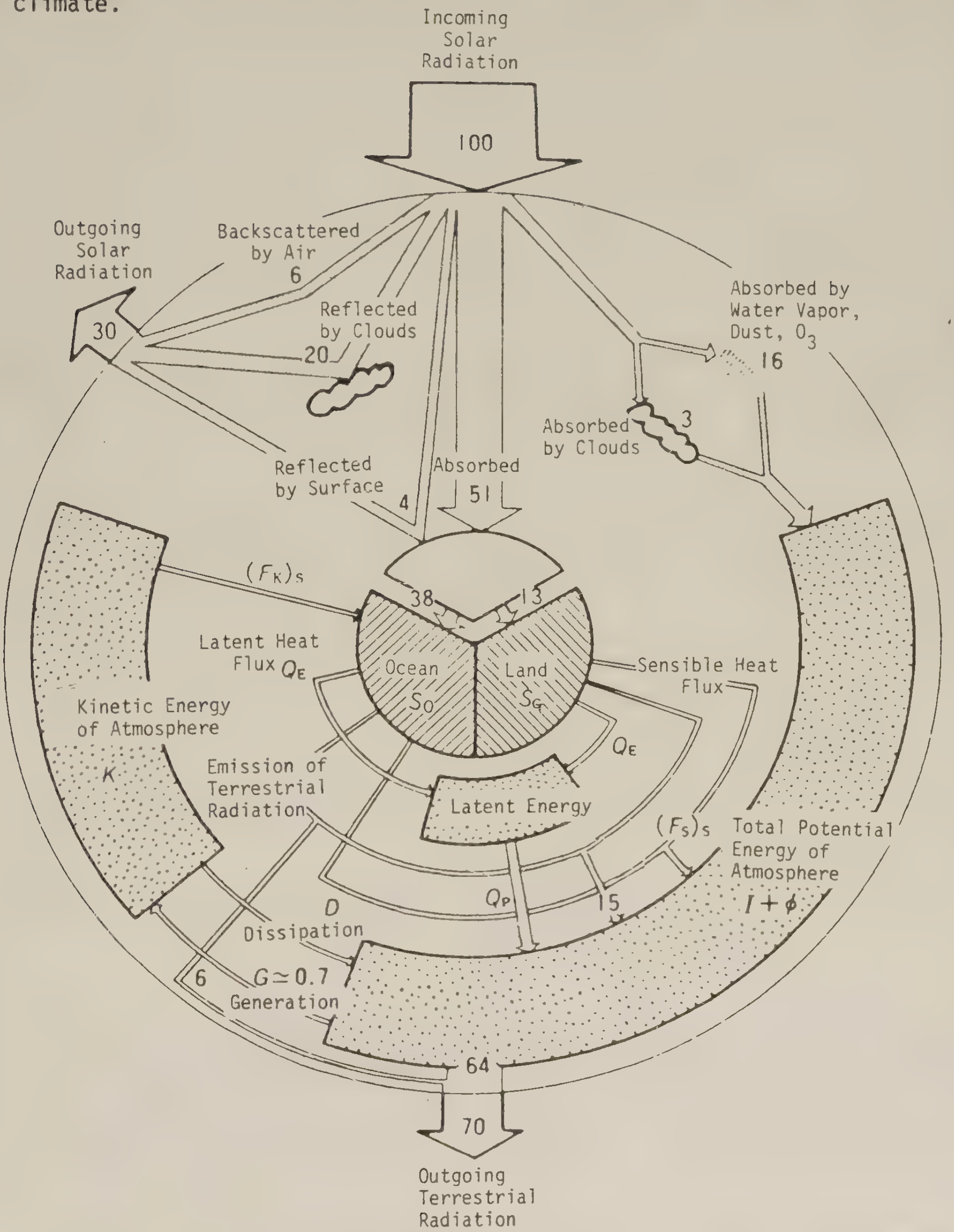
Aparte del fenómeno del El Niño, también se han estudiado las conecciones entre otras anomalías de la temperatura superficial del mar y la circulación anómala de la atmósfera, y se han descubierto correlaciones significativas entre éllas en áreas y épocas partículares.

Varios investigadores han reportado estudios teóricos y númericos relacionados con las anomalías de la temperatura superficial del mar. Estos investigadores están de acuerdo en que la anomalía de la temperatura superficial del mar a bajas latitudes tiene importancia en producir una respuesta significativa a través de la atmósfera global. Algunas conecciones encontradas en el fenómeno de El Niño han sido confirmadas por experimentos númericos recientes usando el modelo global atmósferico.

Los estudios mencionados anteriormente nos proporcionan ejemplos de que los pronósticos mensuales y estacionales son factibles para áreas seleccionadas bajo circunstancias partículares, sí es que las anomalías de la temperatura superficial del mar son conocidas con anterioridad. De momento, se considera que una forma muy directa de desarrollar un sistema de corto alcance para pronosticar el clima es mediante la extensión de modelos usados para la simulación de la circulación global atmósferica o por las predicciones del clima de corto o medio alcance, aun cuando algunas mejoras en el modelo pueden ser necesarias. Entre estas se incluyen las mejoras en la descripción de los fenómenos físicos en la superficie y los intercambios de temperatura turbulentos, la humedad y el momentum en la superficie.

INTRODUCTION

Ocean influences the atmospheric global circulations both thermally and dynamically. The source of energy that drives the atmospheric global circulations is the solar energy. This does not mean that the atmosphere receives energy directly from the sun. Actually, the earth's surface is the main absorber of the solar energy. Fig.1 shows schematically how energy flows within the atmosphere. The incoming solar energy flux is normalized as 100. About 30 is returned back to space without being absorbed by the earth or the atmosphere, and 70 is absorbed by either of them. The figure shows that about 70% of the absorption takes place at the earth's surface, and that the energy is transferred from the earth's surface into the atmosphere through sensible and latent (water vapor) heat fluxes due to turbulent motions and through the terrestrial radiation. About 70% of the earth's surface is covered by the ocean, and the ocean absorbs the solar energy more efficiently than the land surface. In this sense, the ocean is a very important agent that determines the present climate.



Incoming Solar Radiation
100
Outgoing Solar Radiation
30
Backscattered by Air
6
Reflected by Clouds
20
Absorbed by Water Vapor, Dust, O3
16
Absorbed by Clouds
3
Reflected by Surface
4
Absorbed
51
(FK)s
38
13
Latent Heat Flux QE
Ocean
So
Land
SG
Sensible Heat Flux
QE
Kinetic Energy of Atmosphere
K
Emission of Terrestrial Radiation
Latent Energy
(Fs)s
Total Potential Energy of Atmosphere
I + ϕ
D
Dissipation
QP
15
6
G ≃ 0.7
Generation
64
70
Outgoing Terrestrial Radiation

Figure 1: A schematical figure to show energy flow within the earth's atmosphere. Incoming solar radiation (338 w/m2) is normalized as 100. All the energy fluxes are expressed in the normalized unit.

The major physical elements and feedback processes of the coupled atmosphere-ocean system is shown in Fig.2. Evaporation (latent heat flux) from the ocean surface supplies water vapor to the atmosphere. Latent heat is transformed into sensible heat when condensation takes place, and water goes back to the surface. Usually the place of condensation differs from that of evaporation due to atmospheric motions. Therefore the place where the atmosphere is heated through condensation differs from the place where the surface loses its energy through evaporation. Both evaporation and condensation also cause salinity change, and thus density change, within the ocean.

Sensible heat flux through the ocean surface causes temperature change in both the atmosphere and the ocean. Because of the big difference in the thermal inertia between them, the temperature change in the sea surface temperature (SST) is usually small compared to that in the surface air. When the ocean surface is being heated, the shallow upper layer of the ocean is effectively heated due to the stable stratification, and the SST increases fairly rapidly. On the other hand, when the ocean surface is being cooled, downward convection takes place, mixing a relatively thick layer, and changing the SST only slightly.

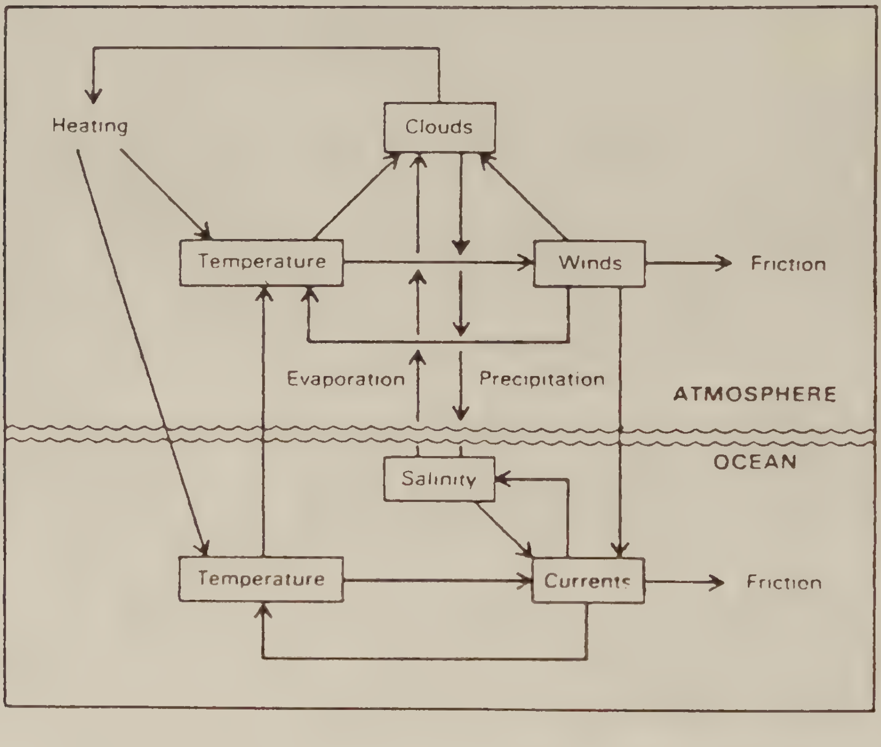


Figure 2: The major physical elements and feedback process of the coupled atmosphere-ocean system. (Taken from Gates, W.L., 1976, Bull. Am. Meteorol. Soc., 57:542)

Global motions within the atmosphere are initiated by the non-uniform heating in the horizontal direction due mainly to geometry and non-uniform topography. The atmospheric global circulations thus initiated transport airmass, energy (or temperature), water vapor and momentum within the atmosphere. Oceanic circulations are initiated not only by the non-uniform density distribution in the horizontal direction caused by heating and salinity change but also by the wind stress at the ocean surface or the momentum transfer through the surface, and transports mass, energy and momentum within the ocean.

The transports of energy and momentum from the earth's surface to the atmosphere due to turbulent motions are given by the following empirical forms:

$$F_s = \rho C_D |\mathbf{V}_s| (S_g - S_s) \tag{1}$$

$$F_W = \gamma \rho C_D |\mathbf{V}_s| L (q_g^* - q_s) \tag{2}$$

$$\mathbf{F_V} = - \rho C_D |\mathbf{V}_s| \mathbf{V}_s \tag{3}$$

F_s, F_W and $\mathbf{F_V}$ are the sensible heat flux, the latent heat flux and the momentum flux vector respectively, ρ: the density of the surface air, C_D: the drag coefficient, $|\mathbf{V}_s|$: the amplitude of the surface wind $\mathbf{V}_s$, S_s: dry static energy (enthalpy + geopotential) of the surface air, S_g: dry static energy of the earth's surface, L: the latent heat of vaporization, q_s: the mixing ratio of the surface air, q_g^*: the saturation mixing ratio of the earth's surface, γ: the factor which depends on the ground wetness. It is noted that no direct information about the oceanic surface currents enter in Eq.(3). This is because the intensity of the surface current of the ocean is much smaller than the atmospheric wind speed. Therefore, changes (or anomalies) in the ocean surface conditions are not recognized by the atmosphere through the dynamical link well, but through the thermal link. On the other hand, changes (or anomalies) in the atmosphere are recognized by the ocean through the dynamical link rather than through the thermal link. This is because the thermal relaxation time of the ocean is longer then the dynamical response time scale of it, due to the large thermal inertia of the ocean.

The changes in the atmospheric circulations are caused by many other processes, for example through interactions with the surface boundaries other than ocean (bare land, snow and ice), through changes in the atmospheric compositions which cause changes in the radiative heatings, such as CO_2, aerosols and so on. These changes may further trigger changes in the oceanic circulations also.

In this paper, a brief summary will be given on the influence of the ocean on the mean atmospheric circulations, and on the observational links between the SST anomalies (SSTA) and the anomalous atmospheric circulations (AAC). Then some theoretical and numerical model studies concerning the influence of the SSTA on the AAC are reviewed. Whether those anomalies are predictable or not is a very important and also a very interesting problem. Present views on that problem will be given in a later section.

THE OCEAN'S ROLE IN THE MAINTENANCE OF CLIMATE

Ocean is distributed non-uniformly on the globe. Therefore geographical differences in the seasonal variations of the circulation may be viewed as a measure of oceanic influence on the seasonal cycle. For example, the annual amplitude of surface air temperature shown in Fig.3 confirms the widely-held impression that the seasonal variations are much less over ocean than over land. This seasonal modulation by ocean is recognized also in other statistics of circulations, such as pressure, wind, precipitation and cloudiness.

Dynamically, the oceanic surface is smoother than the land surface. Therefore the wind speed can be larger near the oceanic surface than near the land surface, if other conditions are the same. The zonally averaged sea level pressure is shown in Fig.4. for both January and July. One of the most notable features of the figure is a large pressure gradient in the north-south direction around 50°S in both months. The latitude zone just coincides with the position of circum-antarctic oceanic belt, where the zonally averaged westerly wind at the surface is the strongest. The zonally averaged wind is approximately connected with the zonally averaged mass distribution through the following geostrophic wind balance:

$$f[u] = - \frac{1}{[\rho]} \frac{\partial [p]}{a \partial \varphi} \tag{4}$$

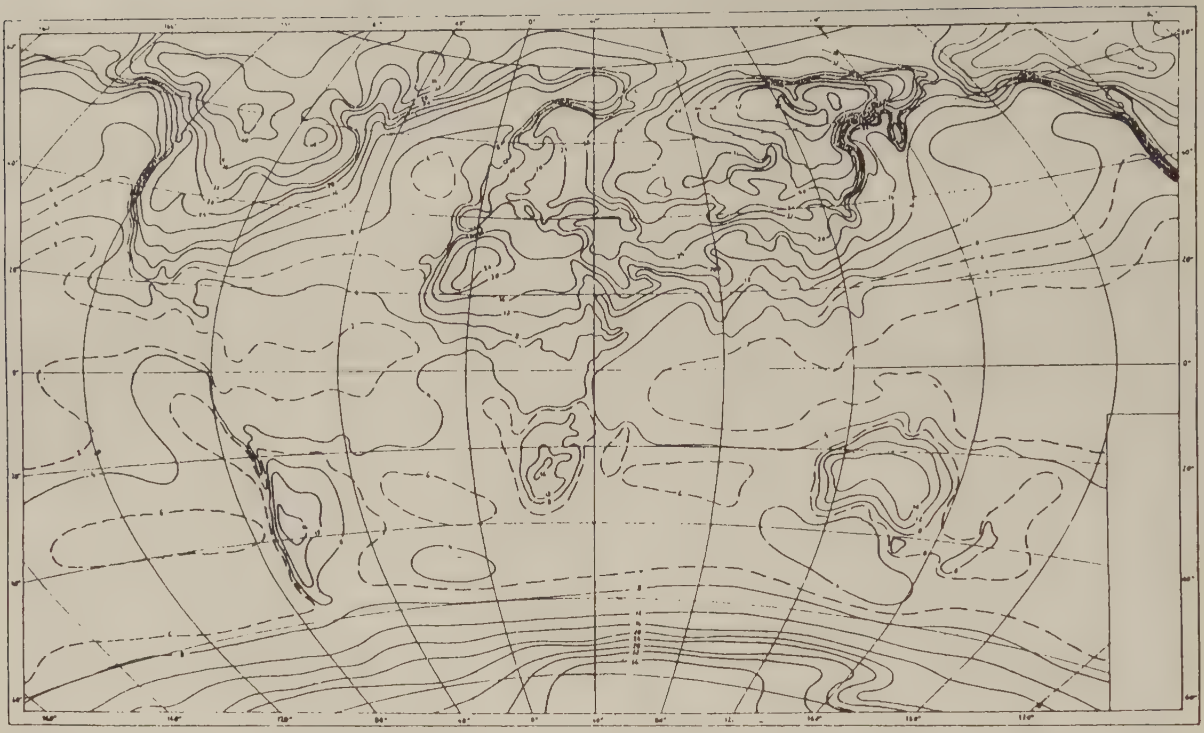


Figure 3: The global distribution of annual amplitude of surface temperature (^{0}K), with the solid line drawn every $4^{0}K$. (Taken from Monin, A.S., 1976, "The physical basis of climate and climate modelling," GARP Pub. Ser. N^{0} 16).

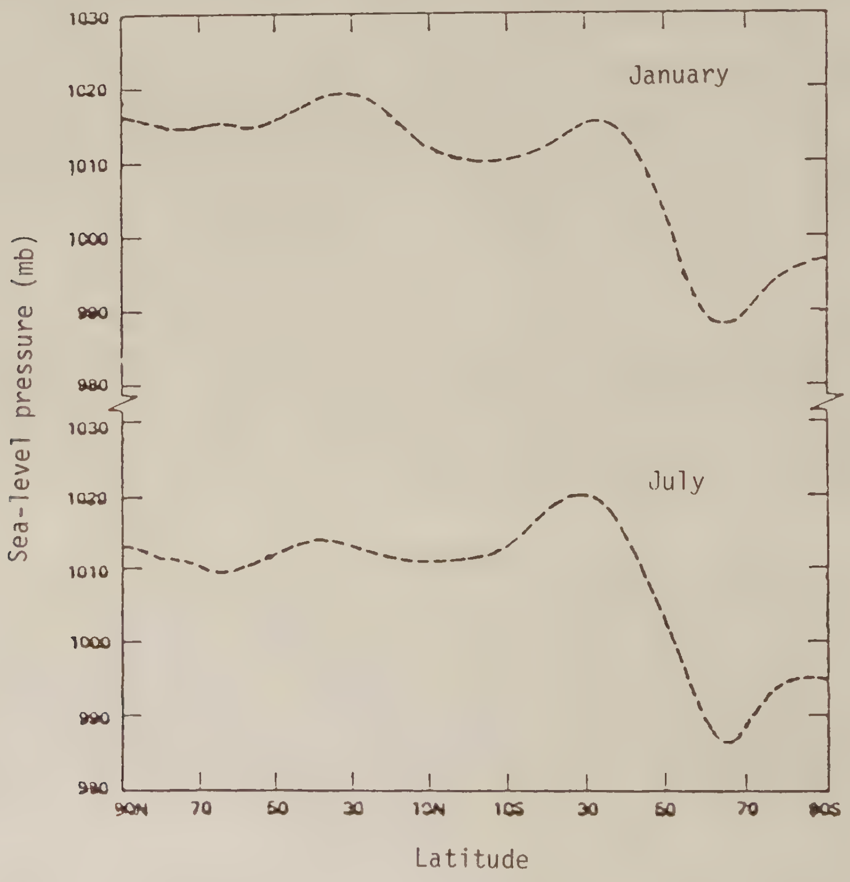


Figure 4: The zonally averaged sea level pressure (mb) for January and July.

where $[u]$ is the zonally averaged eastward wind, $[p]$: the zonally averaged pressure, $[\rho]$: the zonally averaged air density, f : the Coriolis factor $(=2\Omega\sin\varphi)$, Ω : the rotation rate of the earth, φ : latitude, a: the radius of the earth. Therefore we may explain the feature noted above as a dynamical effect of the ocean.

More quantitative study has been presented by Oort and Vonder Haar (1976), with respect to ocean's contribution to the total energy balance of the atmosphere-ocean system. They estimated the seasonal variation of the oceanic heat flux required in the northern hemisphere to maintain an overall balance in the system. The rate of heat storage in both the atmosphere and the ocean is determined based on observational data and is shown in Fig.5 (a) and (b), respectively. The rate of atmospheric heat storage reaches a maximum in May at high latitudes, while the oceanic heat storage rate is a maximum in June in middle latitudes. Somewhat larger heat storage rate and a more complicated meridional and seasonal structure in the ocean are also noted, compared to that in the atmosphere. In mid-latitudes, the oceanic heat storage rate is approximately in phase with the net radiational heating rate and serves to reduce the seasonal contrast by storing heat in summer and releasing it in winter. While near 15°N, the ocean exhibits a maximum storage in spring and a minimum in fall. This behavior is apparently related to seasonal variations of low-latitude upwelling.

Fig.6 (a) and (b) show the seasonal variation of the meridional heat flux in both the atmosphere and the ocean for the northern hemisphere. The flux in the ocean is obtained as a residual of the energy budget equation. A strong northward heat flux is found in winter in the atmosphere, while the oceanic heat flux exhibits a strong semi-annual variation, with maximum northward heat flux in spring and fall in the sub-tropics and southward flux in winter and summer in higher latitudes. In the tropics, an intense southward heat flux occurs in summer, contributing to reduce the global-scale latitudinal contrast of temperature. The amount of heat flux reaches as much as 8×10^{15} W during August, the maximum heat flux found in the atmosphere-ocean system. Although some errors may be inevitable in residuals, Ooort and Vonder Haar clearly demonstrate that the ocean is at least as important as the atmosphere in satisfying the heat transport requirement of the atmosphere-ocean system.

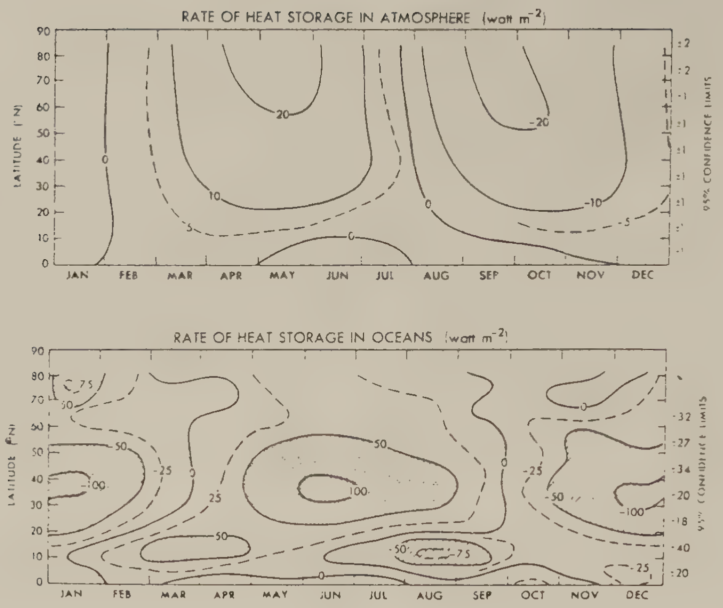


Figure 5: Rate of heat storage (W/m^2) in the atmosphere (a) and in the ocean (b). (Taken from Oort and Vonder Haar, 1976).

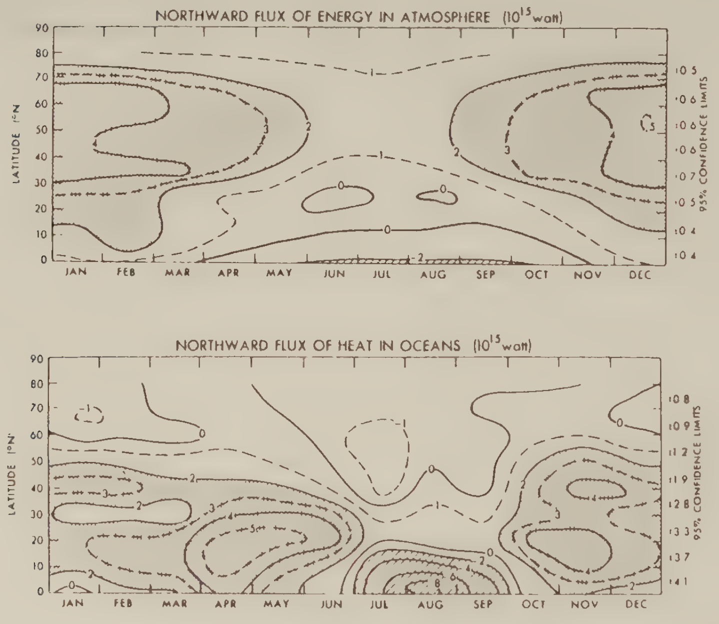


Figure 6: Northward flux of energy (10^{15}W) in the atmosphere (a) and in the ocean (b). (Taken from Oort and Vonder Haar, 1976).

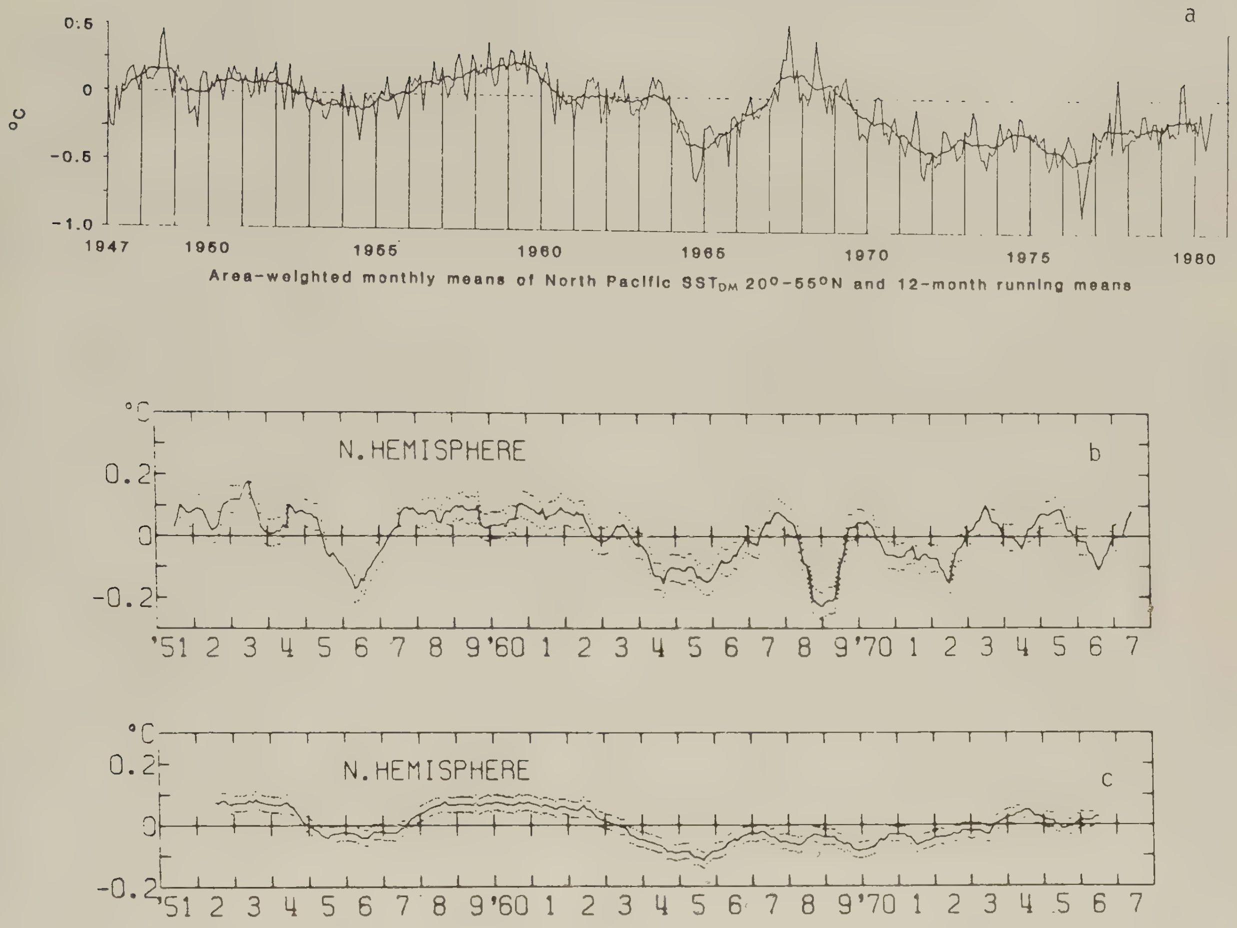


Figure 7: (a) SST deviations from the 1947-1966 mean (dashed line) for the North Pacific in the region 15° to 60°N and 130°E to 110°W. Thin lines connect monyhly anomalies; the thick curve shows the 12-month running means. (Taken from Namias and Cayan, 1981).

(b) 12-month and (c) 36- month running means of the surface air temperature deviations averaged over the northern hemisphere (solid line). The two dotted curves represent the 95% confidence limit for the error. (Taken from Yamamoto and Hoshiai, 1979).

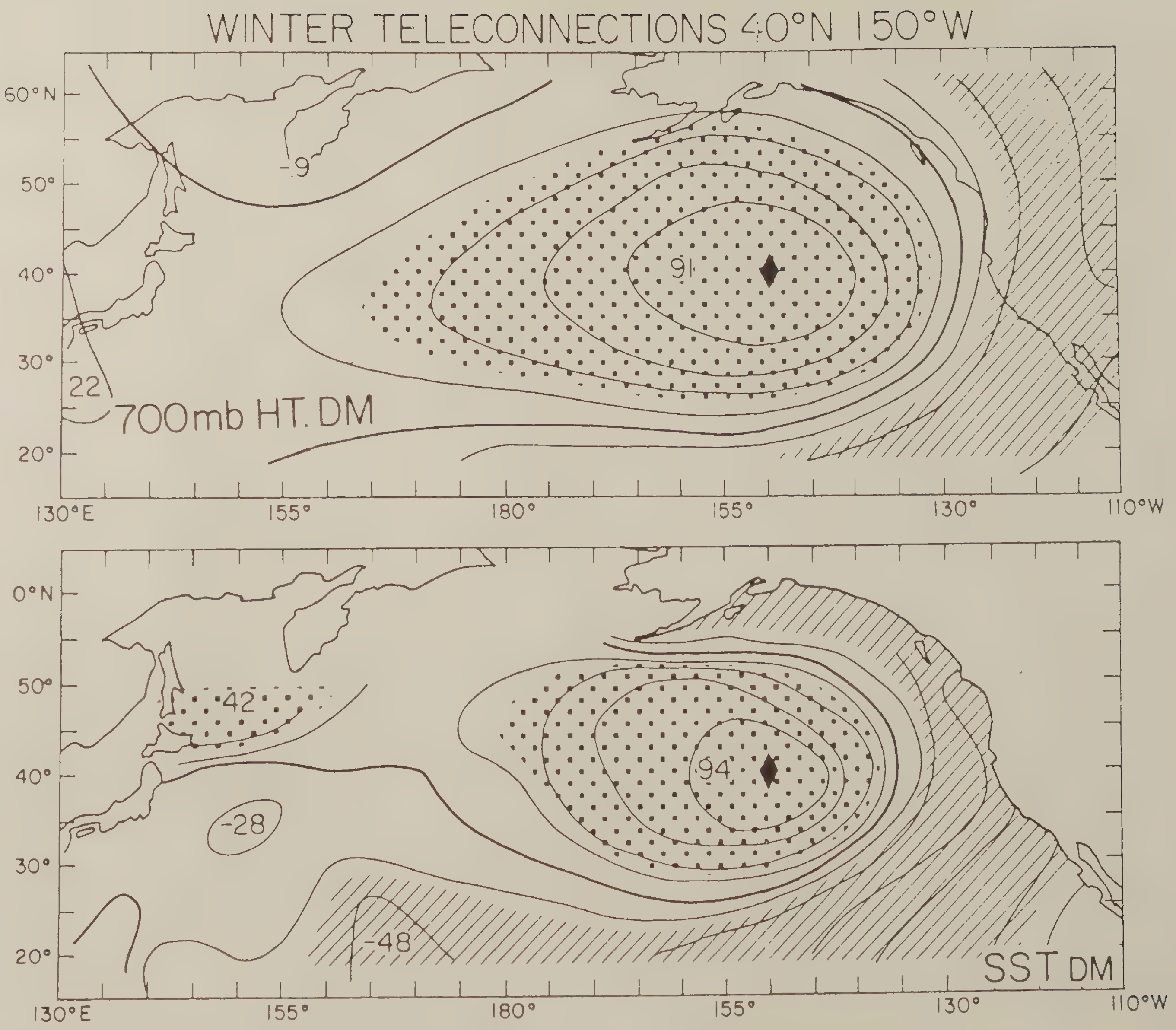

WINTER TELECONNECTIONS 40°N 150°W
700mb HT. DM
SST DM
91
-9
22
94
42
-28
-48
60°N
50°
40°
30°
20°
0°N
130°E
155°
180°
155°
130°
110°W

Figure 8: Cross-correlations of 700mb height (top) and sea level pressure (bottom) with the values at the point (40^0N, 150^0W) for winter. (Taken from Namias, 1982).

NON-SEASONAL CHANGES OF SST AND ATMOSPHERIC CIRCULATIONS

It may be convenient to group studies into four categories, i.e., changes in the hemispheric scale, the changes within the mid- and high-latitidues, the changes within the tropics and the teleconnection between the tropics and the extratropics.

The changes in the hemispheric scale

Namias and Cayan (1981) have shown the existence of interseasonal and interannual changes in the averaged SST departures from the 1947 - 1966 mean SST for the North Pacific in the region 15° to 60°N and 130°E to 110°W. The region corresponds to 20% of the hemisphere. In Fig.7(a) are shown monthly values and their 12-month running means. In the figure, the low frequency signal of the North Pacific SST is quite clear, having periods of several years. The largest anomaly within that period is almost as much as 0.5K over the bulk of the North Pacific.

Changes in the atmospheric temperature have been studied by many workers (Yamamoto et al., 1975; Angell and Korshover, 1977, 1978; Yamamoto and Hoshiai, 1979, etc.). They have shown the existence of interannual changes of atmospheric temperature globally as well as hemispherically. Fig.7 (b) and (c), obtained by Yamamoto and Hoshiai (1979), show 12-month and 36-month running means of the surface air temperature deviations over the northern hemisphere. It is interesting to note similar variations between (a) and (b) or (c). This indicates some connections between the SST in the North Pacific and the surface air temperature of the northern hemisphere. From further comparison of those figures, several months' delay, say 6 months, seems to be noted in the peaks of the surface air temperature anomalies.

Regional studies in the extratropics

Many studies have been reported on the behaviours of the SSTA (sea surface temperature anomaly) and of the AAC (anomalous atmospheric circulation) in the extratropics, especially in the North Pacific. Namias (1982) has shown that there is a great deal of spacial coherence in the SSTA, and that the overlying atmospheric anomalies of mid-tropospheric heights go with high (low) SST's and enhanced northerly air currents off the West Coast are associated with cold water, whereas high pressures and southerly current usually go with warm currents.

The coherence of SSTA over the North Pacific with respect to time is studied by Namias and Born (1970) and Walsh and Richman (1981). In Fig.9 are shown the lagged autocorrelations of monthly mean of SST, 700mb height and sea level pressure, which confirm the fact that SSTA's have their presistence time of several months, which is almost an order of magnitude longer than that of anomalies within the atmosphere. The seasonal dependence of the persistence of SSTA has also been clarified. Fig.10 shows lagged autocorrelations of SSTA, based on the first five EOF (empirical orthogonal function) modes of SSTA, obtained for each season centered on January, April, July and October (Walsh and Richman, 1981). Notice that seasonal persistence is largest when winter (January) is antecedent, and that the persistence does not decrease monotonically with lag. Persistence from January actually increase monotonically with lag. Persistence from January actually increases between lags of 9 and 12 months. Namias and Born has suggested that the warm and shallow mixed layer formed in the upper part of ocean in summer might temporarily shield the SSTA, causing low correlations during that season. Relatively high correlation in the persistence from April between lags of 6 and 10 months may be due to the same mechanism.

Because of the persistent nature of the SSTA mentioned above, and because of sizable effects of the SSTA on the atmospheric global circulations, SSTA is considered as one of the most important predictors of monthly or seasonal predictions (or short-range climate prediction). Namias (1968, 1969, 1971, 1972) pioneered in this respect. Namias (1976) showed that the North Pacific SSTA in summer are significantly correlated with the sea level pressure in fall in the area of the Gulf of Alaska and the temperature anomaly in the United State. Davis (1978) indicated that autumn and winter sea level pressure (SLP) anomalies are predictable from prior observations of either SST or SLP over the North Pacific. On the other hand, he found little or no predictability in SLP of other seasons. Concerning the temperature forecast over the United States, many studies (Harnack and Landsberg, 1978; Harnack, 1979; Walsh and Richman, 1981; Barnett, 1981) followed after Namias (1976), showing that predictions of temperature anomaly over North America are feasible for particular seasons and areas, by use of the SSTA in the North Pacific. Highest predictability is shown in winter along the west coast, the southeastern United States, the northern tier of states and southern Canada (Barnett, 1981).

Regional studies in the tropics

In the eastern part of the equatorial Pacific, there are well known interannual fluctuations in SST called El Niño which originally indicated a weak warm coastal current which annually runs southward along the Ecuador coast around the Christmas season (Wrytki, 1975). In scientific fields, the term has now been used not only to indicate more estreme warmings along the Peru-Ecuador coast which occur every few years, but also to encompass the larger-scale features of the warming event along the equator as well as the South American coast.

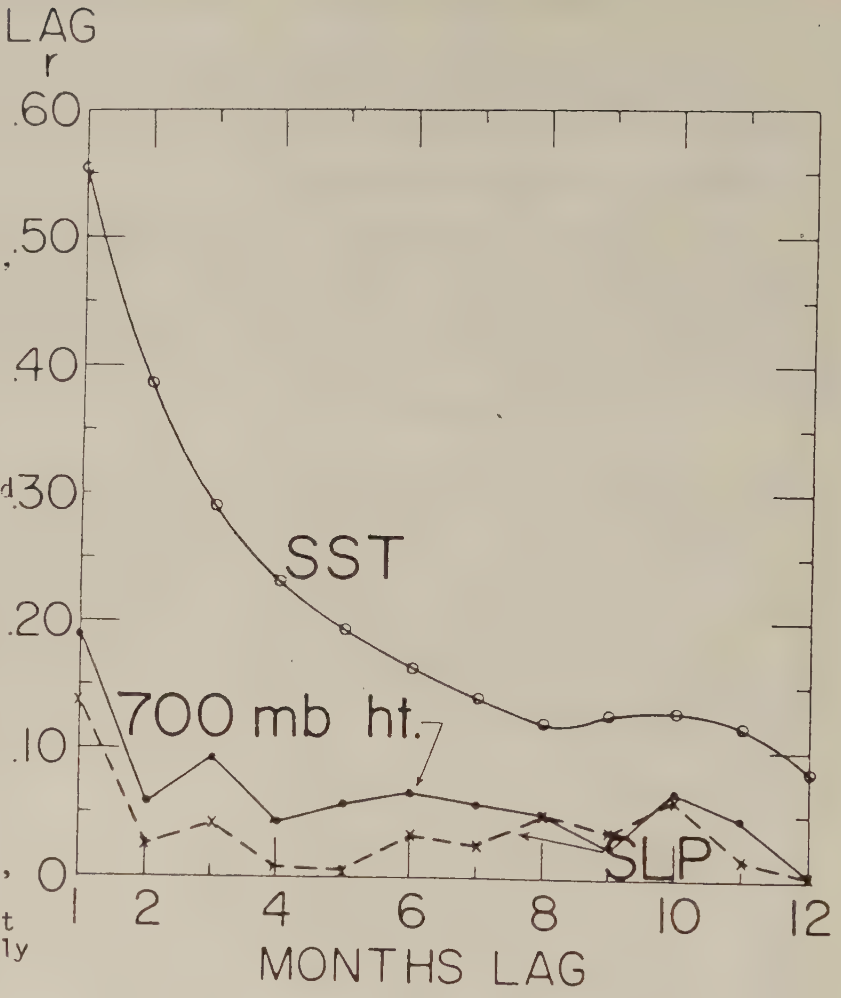


Figure 9: Lagged auto-correlations of values for monthly mean of SST, 700mb height and sea level pressure (SLP) covering the North Pacific (north of 20^{o}N) based on data covering from 1947 to 1966. (Taken from Namias and Born, 1970).

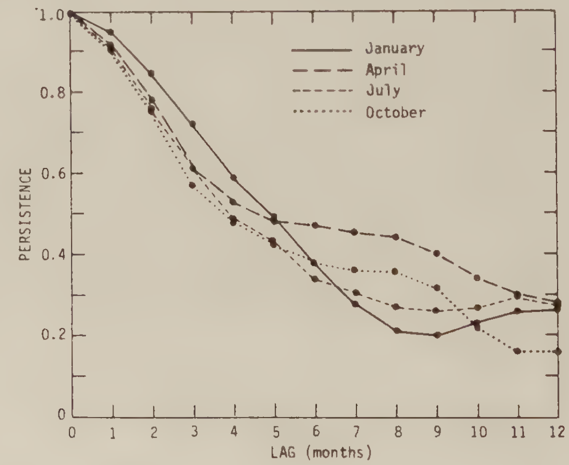


Figure 10: Lagged auto-correlations for seasonal mean of SST centered on January, April, July and October covering the North Pacific. Each dot represents a weighted sum of the auto-correlations of the first five EOF SST amplitudes (3-month running mean). (Taken from Walsh and Richman, 1981).

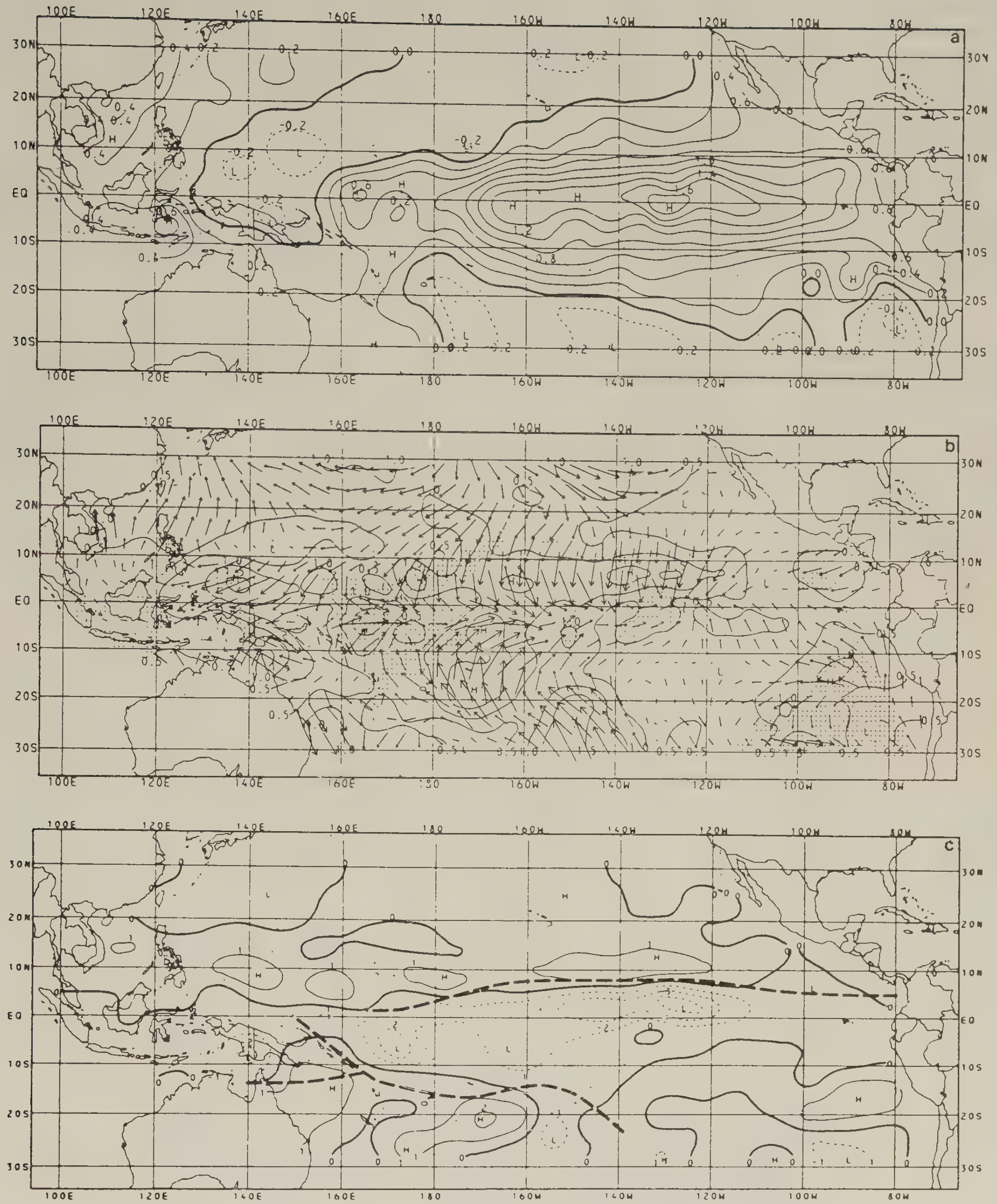

a
b
c
100E
120E
140E
160E
180
160W
140W
120W
100W
80W
30N
20N
10N
EQ
10S
20S
30S

Figure 11: Mature phase anomaly composite (average for December-February following El Niño). Top: SSTA (°K) middle: surface wind anomaly (m/s), bottom: divergence of surface wind anomaly (10^{-6} s^{-1}). (Taken from Rasmusson and Carpenter, 1982).

Rasmusson and Carpenter (1982) studied the evolution of SSTA, surface wind and precipitation patterns throughout El Niño event by compositing data during six warm episodes since 1949. They show that maximam SST anomalies typically occur around April-June (peak phase) along the South American coast, and near the end of the year (mature phase) around 170°W over the equator. Fig.11 shows anomaly composite patterns of SST, surface winds and divergence of the surface winds in the mature phase. Equatorial Pacific east of 160°E is covered by warm SSTA with its peak about 1.6°K. Convergent surface winds extend along the equator over the warm SSTA.

Tropical troposphere is conditionally unstable. Therefore cumulus activity is enhanced over the regions of warm SSTA, causing anomalous heavy rainfall and considerable amount of condensational heating within the atmosphere. Ichie and Petersen (1963) have reported on this for the equatorial central Pacific area and Shukla and Misra (1977) for the Arabian Sea and India.

Considerable warming within the entire tropical atmosphere is observed during El Niño event. Newell and Weare (1976) have shown that average temperature between 700mb and 300mb near 20°N and 20°S is well correlated with the first EOF (empirical orthogonal function) of the Pacific SSTA obtained by Weare et al. (1976) (see Fig. 12). The first EOF is clearly identified as El Niño mode. The correlation between the SSTA and the air temperature is 0.74 when the former leads the latter by 6 months. In Fig.13 is shown similar results obtained by Angell (1981). Horel and Wallace (1981) have also confirmed the spread of the atmospheric response to the SSTA throughout the tropical belt. They show the 200 mb height (i.e. a measure of the troposphere temperature) in the tropics increases during El Niño.

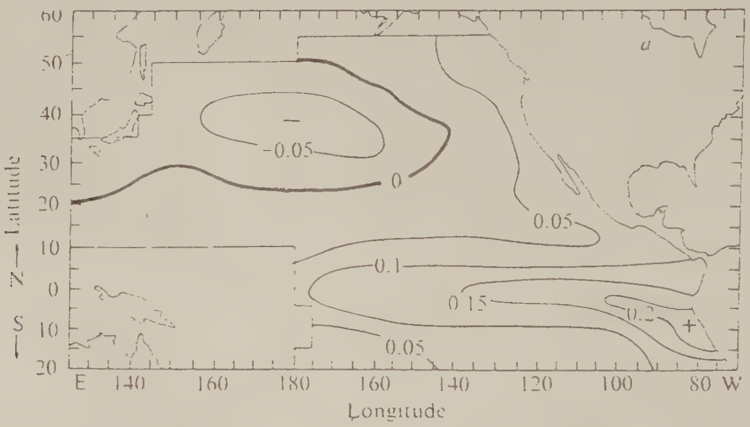


Figure 12: The first EOF (empirical orthogonal function) of SSTA. (Taken from Weare, 1976).

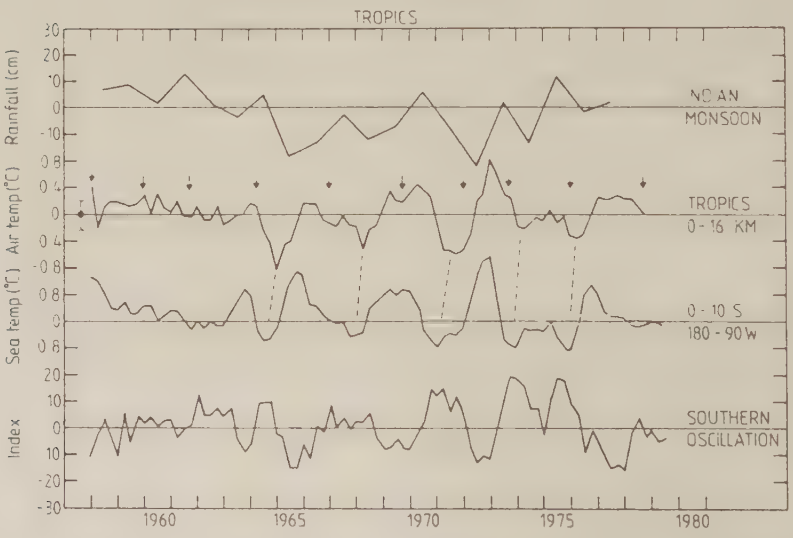
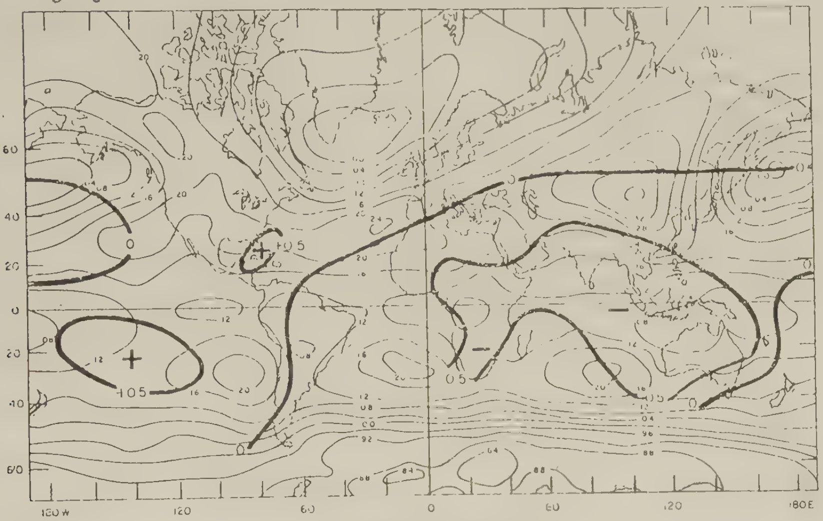


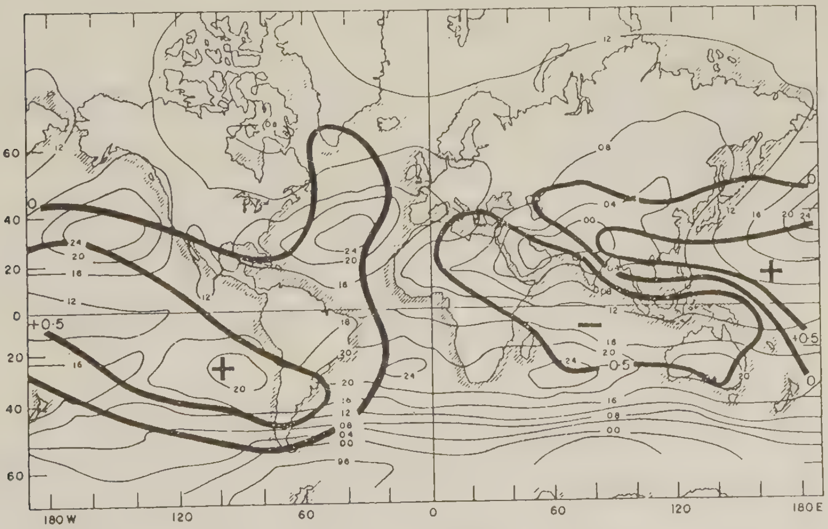
Figure 13: Time variation of the Southern Oscillation Index (normalized pressure difference between Tahiti and Darwin), SSTA (averaged in the region 0° -10°S, 180° -90°W), zonally averaged temperature in 0-16km in the tropics between 30°N and 30°S and summer monsoon (June-September) rainfall for India. (Taken from Angell, 1981).

There is a phenomenon called "the Southern Oscillation (SO)" in the tropics. This is characterized as an interannual seesaw in the sea level pressure between southeast and west equatorial Pacific (or roughly equatorial eastern and western hemispheres) (see Fig. 14). Although the Southern Oscillation was found nearly a century ago, it has started to attract workers again since evidence of a link between the Southern Oscillation and El Niño was found in the late 1960's. Bjerknes (1966, 1969) clearly linked both phenomena by way of changes in the east-west circulation (the Walker circulation). The covariance between the SSTA (0° -10°S, 180° -90°W) or the El Niño mode and the SO index (normalized SLP difference between Tahiti and Darwin) has been demonstrated by many studies (Julian and Chervin, 1978; Angell, 1981; Horel and Wallace, 1981, etc.), as shown in Fig. 13. Negative SO index (relatively low SLP at Tahiti) correlates with the positive SSTA. The correlation is -0.62 with zero time lag. Angell (1981) further shows significant correlation of -0.62 between the SSTA and Indian summer monsoon rainfall 1-2 seasons earlier. The search for the link between the intensity of the Indian summer monsoon, the SST of the Indian Ocean, the SST of the eastern equatorial Pacific and the Indian sea level pressure was tried by Weare (1979).

It is currently accepted that El Niño is a part of the larger phenomenon, i.e. the SO. It is now also likely that the SO is connected further with the Indian monsoon. For thoroughly understanding the trigger mechanism of El Niño, further search for the links between them are highly desired.



(a) December to February



(b) June to August

Figure 14: Correlations of pressures with the Southern Oscillation Index (thick line) for (a) December-February and (b) June-August, and mean sea level pressure (thin line). (Taken from Troup, A.J. 1965. Quart. J. Roy. Meteor. Soc., 91:490)

The teleconnection between the tropics and the extratropics

In the late 1960's, a hypothesis of teleconnection from the equatorial ocean to the atmospheric circulations in the extratropics was presented by Bjerknes (1966, 1969). His insight was based on the anomalous low in the Gulf of Alaska observed in 1967-68 winter, when the anomalous warm water existed in the tropical Pacific from the American coast westward to the dateline. He thought that the sudden introduction of a large anomalous heat into the tropical atmosphere intensified the Hadley circulation locally in association with strong westerly winds and deep low pressure further polewards, and that the deep low had the downwind effect of weakening the Iceland low and setting the stage for a cold winter in northern Europe.

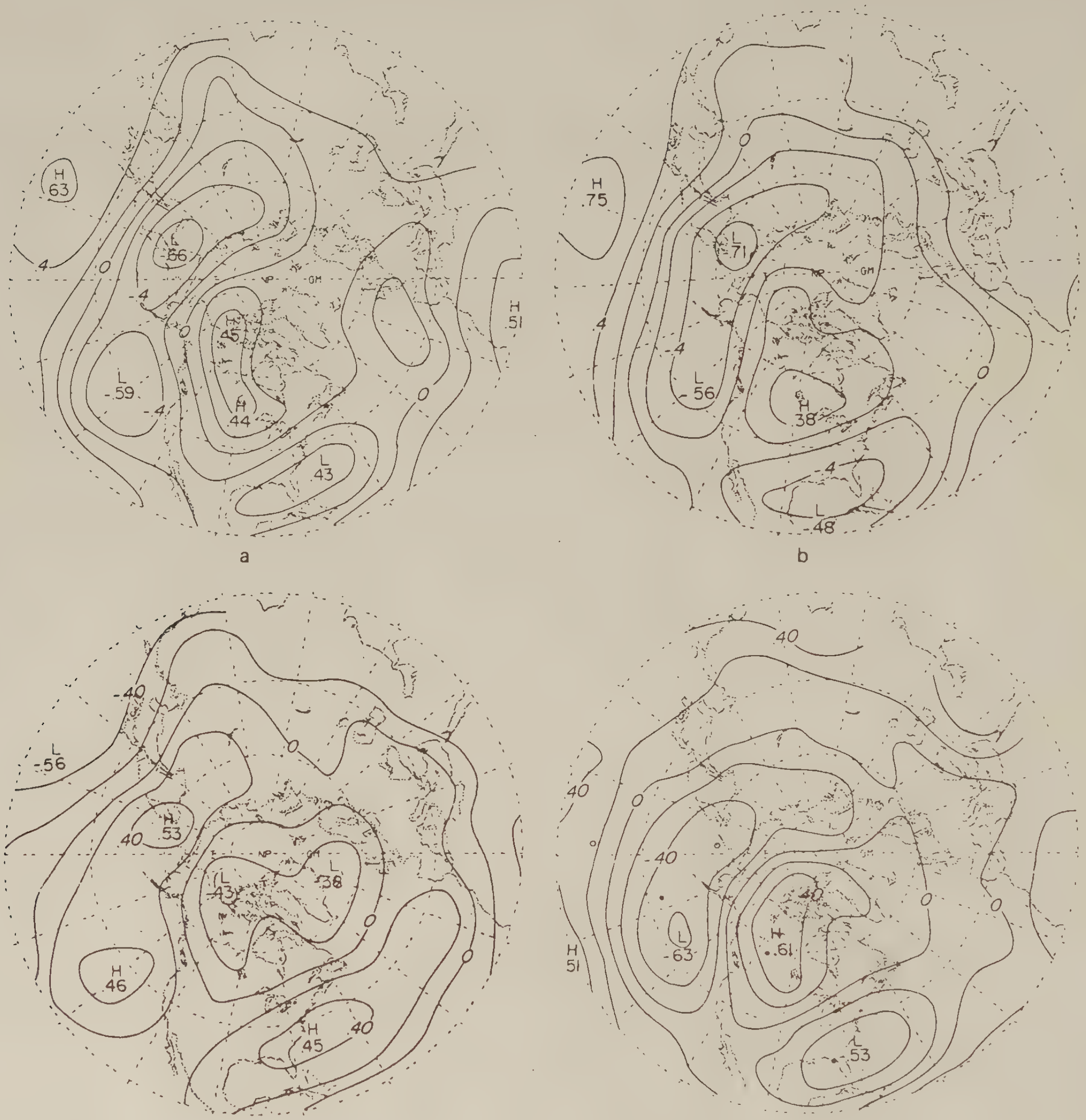


Figure 15: Correlations between 700mb geopotential height at grid points poleward of 20°N and (a) the SST index (based on the average SSTA in the area 5° S-5°N, 180° -80°W), (b) December-February rainfall at Fanning (4°N, 159° W), (c) the Southern Oscillation Index, (d) the tropical 200mb Index (based on geopotential height at Nairobi, Darwin, Nandi, Hilo and San Juan in Dec.-Feb. season). (Taken from Horel and Wallace, 1981).

Bjerknes' hypothesis has now been verified observationally by Horel and Wallace (1981), Angell (1981), Fritz (1982), Barnett (1981) and Arkin (1982). Fig.15 shows the correlation maps between 700mb height and various indices such as the tropical SST index, rainfall at Fanning Island (4°N, 159°W), the SO index and the tropical 200mb height index (Horel and Wallace, 1981). These maps indicate the long distance path of the positive and negative anomalies in various fields. The patterns resemble each other, implying that all factors are mutually interrelated. It is also noted that these maps contain elements of climatologically dominant patterns (Pacific/North American and west Pacific patterns) (Wallace and Gutzler, 1981). Similar teleconnection patterns have been reported by Wright (1979), van Loon and Madden (1981) and van Loon and Rogers (1981), although the links to the extratropical circulations are studied not directly with the SSTA but with the SO index. Trenberth (1976), Angell (1981) and Rogers and van Loon (1982) have pointed out some indications of teleconnection in the southern hemisphere, also.

Barnett (1981) showed that the SSTA in the eastern equatorial Pacific is superior as a predictor of air temperature over the United State to the SSTA in the middle latitudes. Similar results have also been obtained by Angell (1981), showing that the eastern equatorial Pacific SSTA leads the surface temperature anomalies over the United States by two to three seasons. It is interesting that a large portion of predictive skill over the United States comes from the SST in the eastern equatorial Pacific, i.e., the El Niño area.

THEORETICAL AND NUMERICAL MODEL STUDIES RELATED TO THE INFLUENCE OF SSTA ON THE ATMOSPHERIC CIRCULATIONS

As mentioned earlier, atmosphere recognizes anomalies in the ocean surface through the thermal energy flux, not through the momentum flux. Therefore both theoretical and numerical model studies consider only the thermal aspect of the anomalies in the ocean surface, i.e. the SSTA.

Theoretical studies (Webster, 1981, 1982; Hoskins and Karoly, 1981) have shown three types of atmospheric response to the thermal forcing, i.e., the response in the tropics (or diabatic limit), the response in the extratropics (advective limit) and teleconnections through the propragation of Rossby waves.

Atmospheric responses in diabatic and advective limits

We consider forced solutions within the atmosphere to the thermal forcings. Because the movement of the SSTA is usually quite slow, we study stationary responses of the atmosphere to the stationary thermal forcings. Then the governing equations are written as follows:

$$\bar{u}\zeta'_x + \beta v' = f w'_z \tag{5}$$

$$\bar{u}\theta'_x + v'\bar{\theta}_y + w'\bar{\theta}_z = \frac{1}{\rho c_p} Q' \tag{6}$$

Eq. (5) is the linearized form of quasi-geostrophic vorticity equation, which is a good aproximation of the vorticity equation for the slowly varying large-scale motions except in the vicinity of the equator. Eq. (6) is the linearized form of the thermodynamic equation. Elements with the bar and the superscript indicate basic and forced parts respectively. u,v and w are velocities in the eastward (x), northward (y) and vertical (z) directions respectively; ζ, the vertical component of vorticity ($=v_x - u_y$); f, the Coriolis factor; β=df/dy; θ, potential temperature; Q, diabatic heating rate; ρ, density of the air; c_p, the specific heat of the air. The subscripts $_x$, $_y$, and $_z$, indicate derivatives with respect to the subscripted variables.

In the atmosphere, horizontal temperature gradients are small in the tropics compared to that in the extratropical latitudes. Therefore in the tropics, the third term on the left hand side of Eq. (6) is a major term that balances with the diabatic heating term on the right hand side. This balance is termed as "diabatic limit" by Webster (1981). In the extratropics, on the other hand, the first and second terms, especially the second one, are the main terms that balance with the diabatic term. Temperature usually decreases poleward. Therefore equatorward wind transports cold air-mass, which counterbalances with the diabatic heating. This balance is the "advective limit".

The forced steady motions should also satisfy dynamical balance, Eq.(5). In the diabatic limit, convergence ($w'_z > 0$) exists in the lower atmosphere of the heated region. This acts to increase cyclonic vorticity (stretching effect). For the scale of motion (L) larger then $L_c = 2\pi(|u|/\beta)^{1/2}$, the second term on the left hand side of Eq.(5) is dominant over the first one. Thus poleward wind is required to counterbalance the stretching effect. This means a westward shift of cyclonic center relative to the heating center. The first term, under this circumstance, acts in the same sense as the second term in low latitudes where easterly prevails on the average. L is approximately 3,00km at 10° latitude when $|u| = 5$m/s.

In the advective limit, equatorward wind is required over the heated region. This means an eastward shift of cyclonic center relative to the heating center. In the extratropics, westerly wind exists on the average. If we take this into account, the left hand side of Eq.(5) tends to increase cyclonic circulations over the heated region for $L > L_c$, and anticyclonic circulations for $L < L_c$. In order to counterbalance this effect, divergence ($w'_z < 0$) is required in the former case ($L > L_c$), i.e. subsidence in the lower part of the atmosphere in the heated region, and upward motion in the latter case.

Fig.16 shows examples of atmospheric response to the localized thermal forcing in both the diabatic and advective limits. The top figures show the vertical p-velocity maps (negative values indicate upward motions) where the center of the thermal forcing is located at solid circles. Middle and bottom figures show stream function and wind vector at 250mb levels, respectively. These figures confirm the qualitative discussion above.

Teleconnection through the propagation of Rossby waves

Hoskins and Karoly (1981) discussed how barotropic stationary Rossby waves forced at a localized region propagate over the sphere. In their nondivergent barotropic model, forcing of anticyclonic vorticity in a tropical region is considered as an equivalent to thermal forcings in a barotropic model, as a tropical thermal anomaly forces anticyclonic circulation at upper levels through the stretching effect.

They showed that the stationary response of the non-divergent barotropic model to the forcing of anticyclonic vorticity can be explained by the propagation of barotropic Rossby wave activity along the ray path, which is governed by a dispersion relation and

$$\frac{dy}{dx} = \frac{V_g}{U_g} \tag{7}$$

where U_g and V_g are the group velocities of the Rossby wave in x- and y-directions respectively. For a low- latitude source, the ray directs polewards as well as eastwards for long waves. Shorter waves are trapped equatorward of the poleward flank of the jet, resulting in a split of wave trains at this latitude. Fig. 17 shows ray paths from the source at 15° and phases every 180° for wavenumbers indicated by numbers in the figure. The characteristics in the figure are common to the response of a baroclinic model atmosphere to the tropical thermal forcings (Fig.18) and also to the observed teleconnection patterns (see Fig. 15 for example).

It is observationally known that there is a seasonal dependence in the teleconnection between the tropics and the extratropics. Large responses are usually observed in the extratropics of the winter hemisphere. This is due to the high sensitivity of wave propagations to the zonal wind distributions. Easterlies do not allow propagation of stationary waves. Subtropical easterly region extends poleward in summer, providing unfavorable conditions for stationary wave propagations. Webster (1982) confirmed this seasonality with the use of a 2-layer global model.

Studies on the effects of SSTA with the use of numerical atmospheric models

Numerical atmospheric models are widely used in meteorology. In the numerical models, physical variables, such as winds, temperature, mixing ratio of water vapor, surface pressure, etc., are represented in terms of values at grid points distributed in space or in terms of a set of coefficients of some orthogonal functions in space. The time evolution of the variables are determined by numerical time integration of the governing equations (the momentum equation, the thermodynamic eq., the conservation of mass, water vapor, etc.). Numerical models give us a complete data set of variables, which enables us to analyse any phenomena occuring within the model atmosphere. Some of the data may even be such that are usually difficult to measure or impractical to get in global scale. Therefore a reliable numerical atmospheric model is very useful for many purposes.

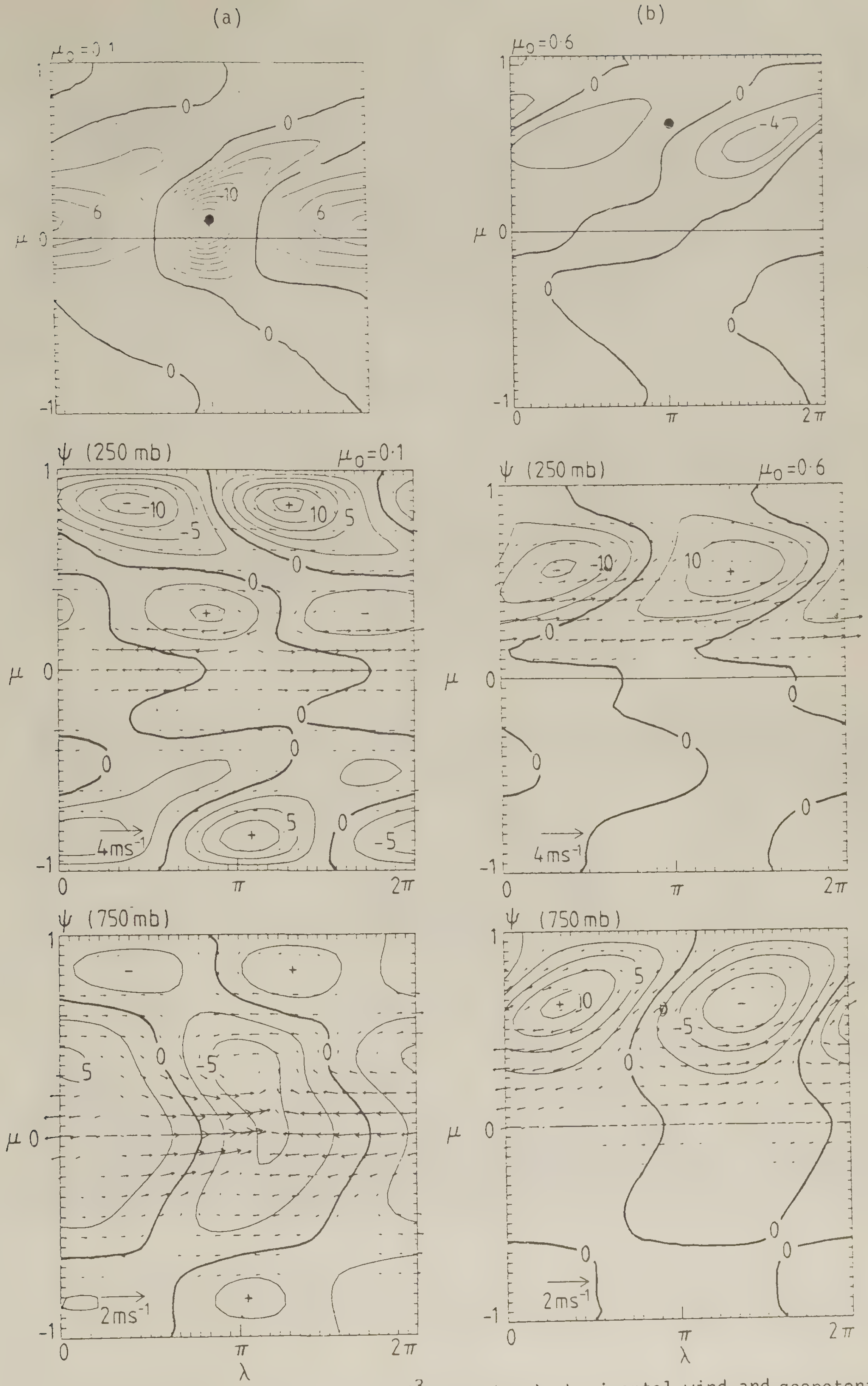


Figure 16: Vertical velocity (unit 10^{-3}Pa/s) (top), horizontal wind and geopotential (unit m) at 250mb (middle) and 750mb (bottom) for the "diabatic limit" case (a) and the "advective limit" case (b). Maximum SSTA is located at (a) 5.7°N and (b) 36.0°N (solid circle in the top figure), respectively. Ordinate indicates sine of latitude. (Taken from Webster, 1981).

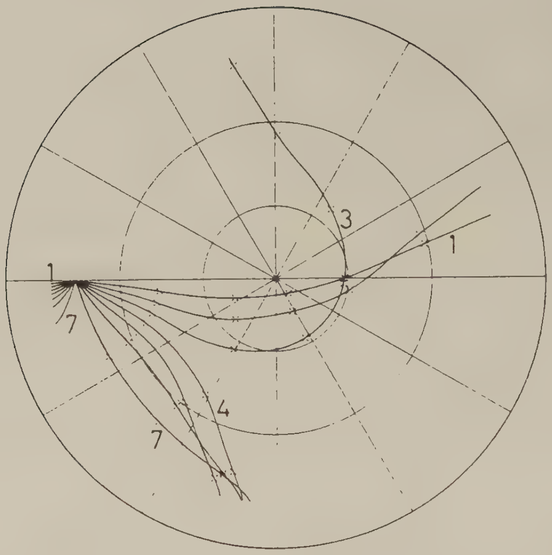


Fig. 17: Ray paths (solid line) and phases every 180^0 (cross) of the barotropic Rossby waves originated from the source at 15^{O}N. Numerals in the figure denote wavenumbers of the waves in the east-west direction. Low wavenumber modes reach high latitudes, while high wavenumber modes are trapped equatorward of the poleward flank of the jet. (Taken from Hoskins and Karoly, 1981).

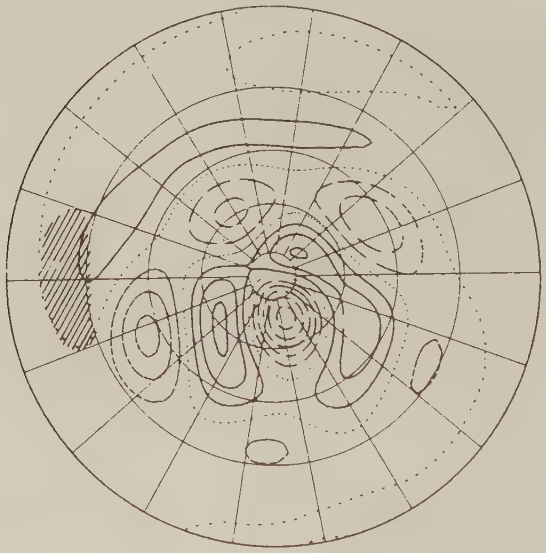


Figure 18: Steady state geopotential solution of a baroclinic model for a deep heat source (shaded area) of its center at 15^o. (Taken from Hoskins and Karoly, 1981).

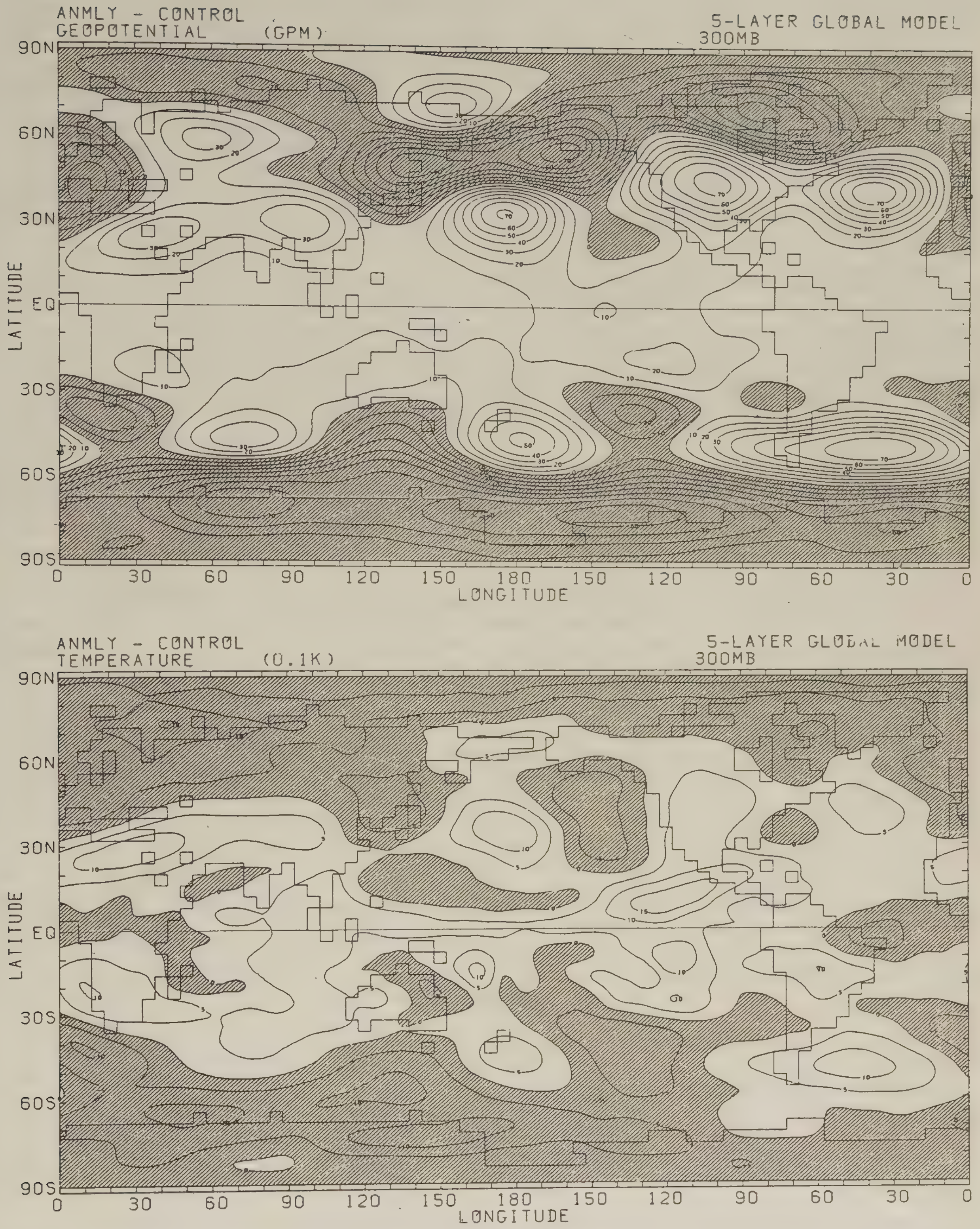

ANMLY - CONTROL
GEOPOTENTIAL (GPM)
5-LAYER GLOBAL MODEL
300MB
90N
60N
30N
EQ
30S
60S
90S
LATITUDE
0
30
60
90
120
150
180
150
120
90
60
30
0
LONGITUDE
ANMLY - CONTROL
TEMPERATURE (0.1K)
5-LAYER GLOBAL MODEL
300MB
90N
60N
30N
EQ
30S
60S
90S
LATITUDE
0
30
60
90
120
150
180
150
120
90
60
30
0
LONGITUDE

Figure 19: Difference of geopotential (top) and temperature (bottom) at 300mb between the runs with and without the SSTA shown in Fig.15. Units are gpm and 0.1K respectively. Negative area is shaded. (Tokioka, Kitoh and Katayama).

The effects of SSTA on the atmospheric circulation have also been studied by use of numerical atmospheric models. Rowntree (1972) studied the Bjerknes' hypothesis, employing 9-level hemispheric model of the atmosphere developed at the GFDL (Geophysical Fluid Dynamics Laboratory, NOAA). Four 30-day integrations were made, two with warm and two with cool tropical east Pacific SST, under January conditions. He obtained, for the warm SST cases, increased rainfall over the central and east Pacific with decreases over the west Pacific and parts of South America, a strong mid-Pacific high near 30°N and a deep Gulf of Alaska low with warm air over much of Alaska and western Canada, with fair agreements with Bjerknes' hypothesis. Changes further downstream depended on the initial conditions. He suggested the importance of using correct tropical SST even for short period numerical predictions in the tropics, and for the prediction in the extratropics extending more than a week. Later a similar problem was also examined by Julian and Chervin (1978).

Recently numerical experiments concerning the effects of mature phase El Niño were performed by Shukla and Wallace and by Tokioka, Kitoh and Katayama, with the use of the GLAS (Goddard Laboratory for Atmospheric Sciences)- and the MRI (Meteorological Research Institue)- global atmospheric models respectively. Both studies adopted the SSTA analyzed by Rasmusson and Carpenter (1982) as a forcing (see Fig.11), and confirmed responses similar to those revealed by observational studies, showing the existence of stationary significant responses in the global extent to the tropical SSTA. Further they clearly confirmed primarily equivalent barotropic nature of the extratropical anomalies, with temperature anomalies and geopotential height anomalies occurring in phase with one another (see Fig.19), again in agreement with observations. The reason why equivalent barotropic (external) Rossby modes are observed as the most dominant anomalies may be explained as that the equivalent barotropic nature of the anomalies allow farther horizontal propagation of wave action than other modes because of no energy dispersions in the vertical direction. The situation may be similar to the long lived propagation of "tsunami" or long waves in the ocean. The model response similar to the SO is also recognized by them. Fig.20 shows the anomalous east-west (Walker) circulations averaged between 10°S and 10°N. In this figure, smaller scale of east-west circulations, reflecting rather smaller scales of SSTA in Fig.15 are superposed on the large-scale circulation corresponding to the SO.

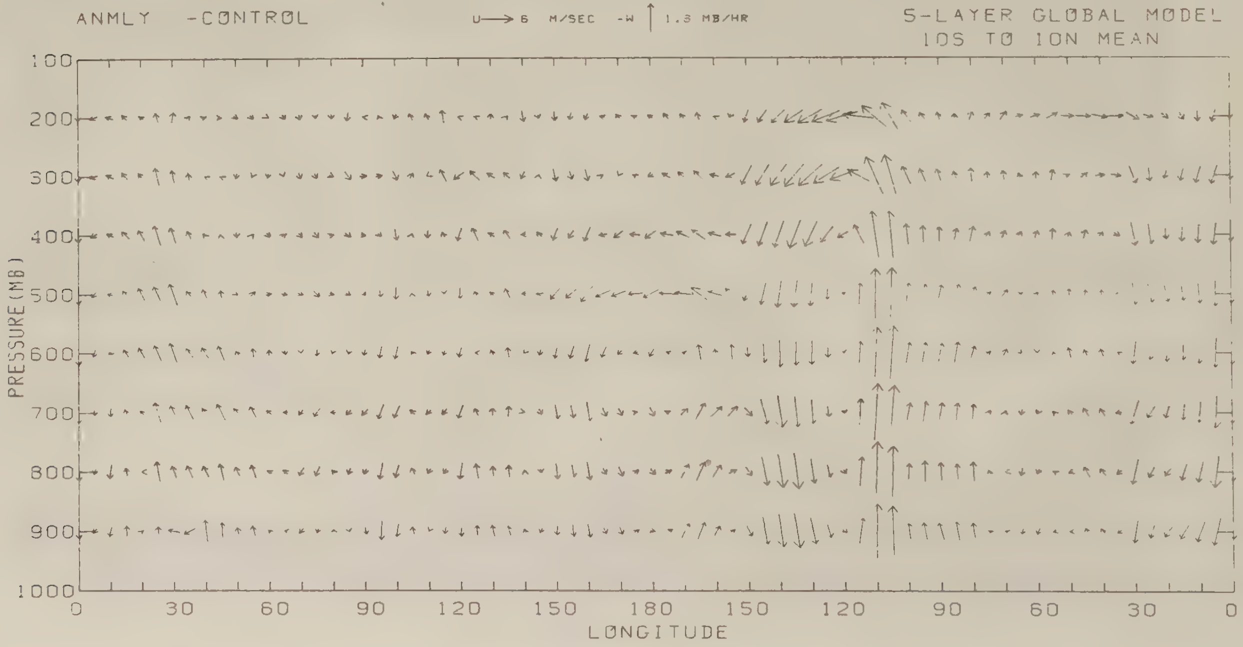


Figure 20: Difference of the east-west circulations between the runs with and without the SSTA shown in Fig.15. The circulations are averaged between 10°S and 10°N. (Tokioka, Kitoh and Katayama)

Concerning the effects of other tropical SSTA's, several studies have been performed. Rowntree (1976) studied the case of the north tropical Atlantic SSTA, Shukla (1975) the Arabian sea anomaly, Moura and Shukla (1981) the tropical Atlantic anomaly, and Keshavamurty (1982), the eastern, central and western Pacific anomalies in the June - August season. These studies have demonstrated the sizable effects of SSTA on the atmospheric part in each situation.

Houghton et al. (1974), Chervin et al.(1976), Kutzbach et al. (1977) and Chervin et al. (1980) studied the atmospheric response to the extratropical SSTA with the use of the northern hemisphere NCAR (National Center for Atmospheric Sciences) model, and showed that a statistically significant signal can be detected in the immediate vicinity of large SSTA, but that teleconnections of the signal further downstream can be identified only with a small statistical confidence. This is quite contrasting to the cases of equatorial SSTA forcings, where significant atmospheric responses are detected in the extratropical latitudes of winter hemisphere as well as within the tropics.

Simpson and Downey (1975) studied the atmospheric response to the SSTA centered at 45^oS 180^oE with the use of the southern hemisphere model. They showed that even the atmospheric response in the immediate vicinity of the anomaly is not systematic. Recent global model study by Manabe and Hahn (1981) showed that the model with a fixed SST reproduces the "observed" variability of pressure patterns in mid-latitudes, but the model variability in the tropics is much less than the observed one. All these studies support the view that the SSTA effects in the extratropics are difficult to identify with confidence over the natural noise level, and also do not contradict with the results by Webster (1981, 1982) that the SSTA in the advective limit has less effects on the atmosphere than that in the diabatic limit.

PREDICTABILITY OF SHORT-RANGE CLIMATIC FLUCTUATIONS DUE TO SSTA

Feasibility

As briefly discussed in the Introduction, there are many physical processes which take part in determining the present climate (see Fig.1 and 2). Important processes which contribute to the changes of atmospheric circulations vary with the time scale dealt with. Energy is converted from total potential energy to kinetic energy at the approximate rate of 0.7 in the normalized unit in Fig.1. This rate provides us a time scale of about five days to build up (or dissipate) the kinetic energy of the atmosphere. We may define another time scale, i.e. the build-up time of the total potential energy. This time scale is much longer than the time scale of dissipation and is roughly equal to four months. If we consider predictions of large scale flows over the period much less than five days, say 5 hrs, advective processes are very important and energy conversion from the total potential energy to the kinetic energy is negligible. For the one or two days' prediction, we have to consider energy conversions from the total potential energy into the kinetic energy, although the energy supply mechanisms of the total potential energy itself may still be neglected. However, the importance of the proper treatment of diabatic process increases with the increase of the prediction range.

Miyakoda (1982) pointed out that the SST, soil moisture, snow cover and sea-ice are the most important surface boundary forcings for short-range (from monthly to seasonal) climatic fluctuations. As shown previously, the tropical SSTA is effective in producing significant effects on the atmospheric variabilities not only in the tropics but also in the extratropics. The impact of the SSTA depends appreciably on the seasons and the areas and the SSTA can be used as a predictor in the statistical forecasts for particular seasons and the areas, although elaborate statistical approaches have up to now provided only a slight improvement in the forecasting over simple climatological and persistence methods (e.g. Nicholls, 1980; Nap et al., 1981). Because of the great value in any forecast of significance, efforts should be continued to improve and extend the current statistical approaches. Yet, any such improvements from purely statistical approaches are likely to be limited for the following reasons (Dickinson, 1982):

i) Much of the seasonal memory of the climate system is expected to reside in surface variables such as the SST and the soil moisture, whose information is at best imperfectly captured by current schemes that rely largely on conventional meteorological observations.

ii) Another limitation on statistical approaches is imposed by the combination of the short time over which climate data are available, together with the high number of degrees of freedom in the climate system.

At present, it seems to be a straightforward way to develop a forecasting system for the short range climate prediction by direct extentions of the models used for the simulation of the global atmospheric circulations or for the short- or the medium-range weather predictions. Shukla (1981) has carried out two-month atmospheric predictions with the GLAS model from observed initial conditions, but with climatological values for ocean temperature, sea ice, snow and soil moisture. Predictions were repeated three times using randomly perturbed initial conditions. Large scale features of geopotential height were found to have some predictability up to 30 days (see Fig.21). He also pointed out, in comparing the monthly averages of the first and second forecast months, that the variability between forecasts with the same initial state was small compared to the variability between forecasts with different initial states for the first month, but that this was not the case for the second month. In another words, the effect of initial conditions is retained at least up to one month by the model atmosphere. He mentons, based on his results, the possibility of extending predictability beyond one month by improving the model, the initial conditions and the parameterization of physical processes.

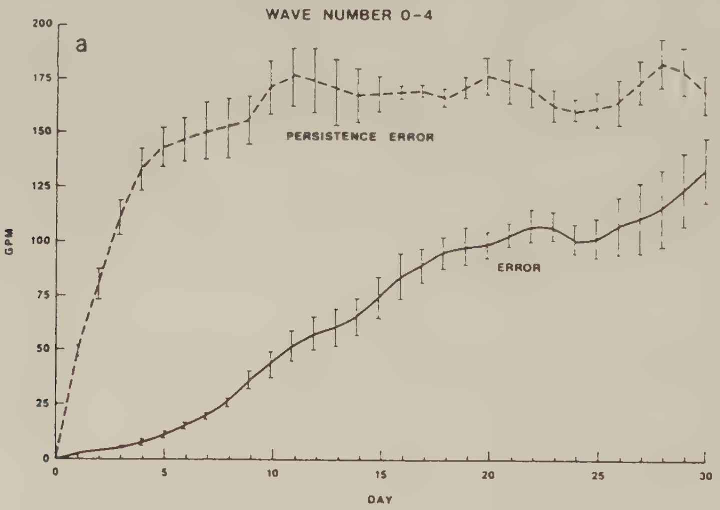


Fig. 21: Root mean square error averaged for six pairs of control and perturbation runs, and averaged for latitude belt 40^{0} -60^{0}N for 500mb geopotential height (gpm) for longitudinal wavenumber 0-4. Dashed line is the persistence error. When the r.m.s. error is less than the persistence error, the model is considered to prossess predictability. (Taken from Shukla, 1981).

Miyakoda et al. (1981) and Sirutis and Miyakoda (1981) have performed other 30-day forecasts with the GFDL model, and tested the effect of improving the parameterization of surface boundary layer and surface turbulent fluxes. They found the model with a sophisticated parameterization gives much better results after 2 weeks than the one with a simpler treatment. Recent numerical experiments by Shukula and Wallace and Tokioka, Kitoh and Katayama mentioned earlier have succeeded in reproducing statistically significant atmospheric responses to the mature phase SSTA of El Niño. These numerical studies give another support to the feasibility of short-range climate prediction, demonstrating the importance of specifying accurate SST in the tropics.

Coupled atmosphere-ocean model

There is evidence that a large part of the low-latitude atmospheric variability is due to boundary forcing anomalies (Shukula, 1981; Manabe and Hahn, 1981, Charney and Shukula, 1981), especially the SSTA. The variations of the tropical SST in turn depend intimately on the wind stress exerted by the trade winds changing the depth of the oceanic thermocline. The characteristic time of large scale interaction between the atmosphere and the ocean extends over the wide range from days to some thousand years. In this sense, climate model should basically be a coupled atmosphere-ocean model.

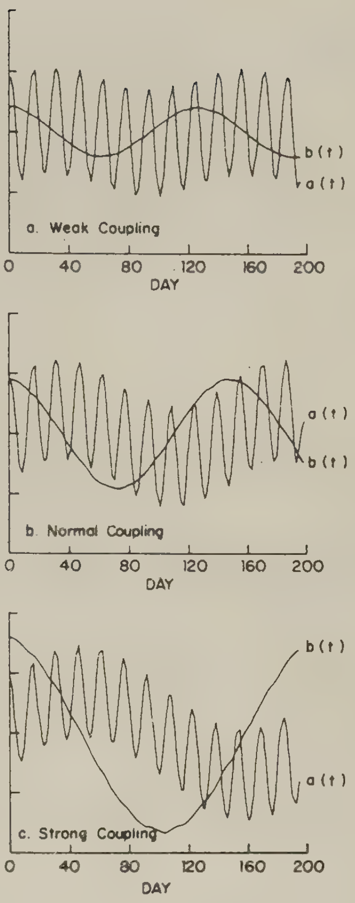


Figure 22: Time variation of the amplitude of the longest wave for the zonal wind a (t) and for the sea level b (t). Ordinate is in arbitrary unit. Short time period seen in a (t) and the long time period in b (t) correspond to those of Mode I and Mode II, respectively. Intensity of the coupling is proportional to $\frac{C_D|V_s|}{D_1}\left(\frac{\rho}{\rho_0}\right)^{1/2}$ where ρ_0 is the density of water and D_1 is the depth of the thermocline. Other notations are the same as in the text. (Taken from Lau, 1981).

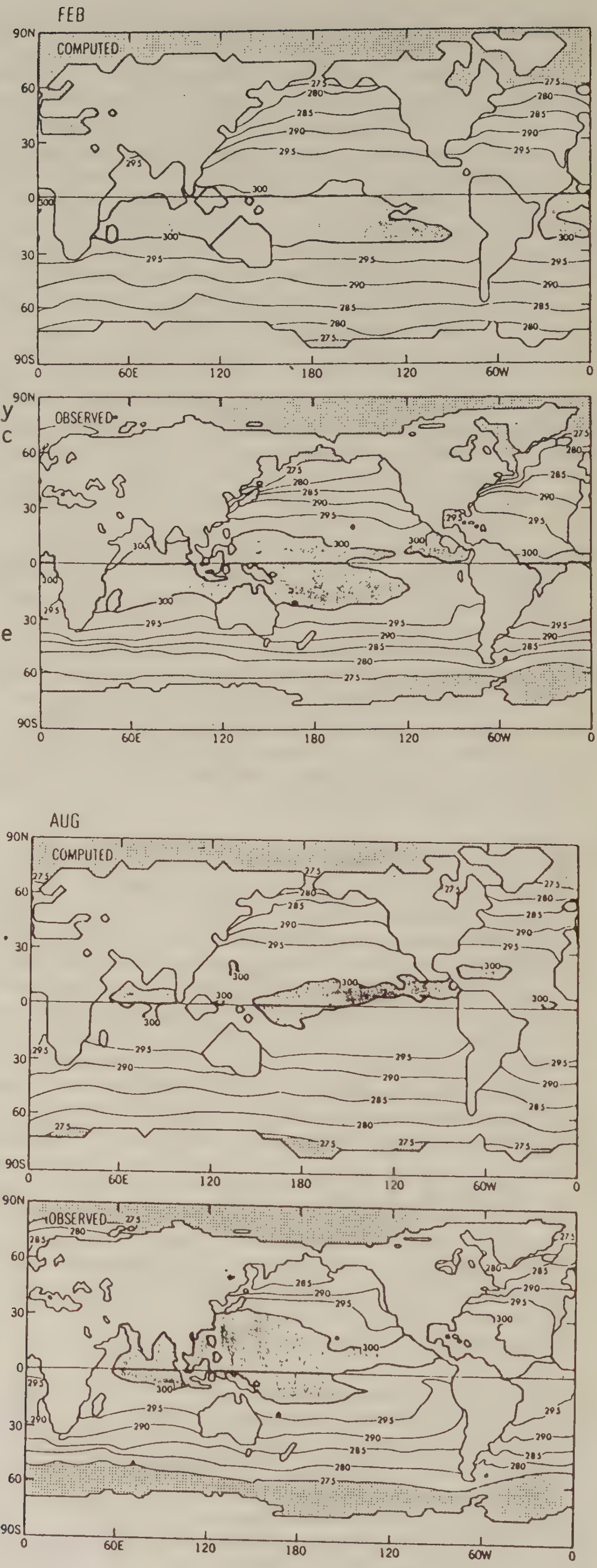
Theory predicts that the time-scale of the dominant process of the ocean highly depends on latitude and that it decreases with the decrease of latitude (Moore and Philander, 1977). The time required for the baroclinic Rossby waves to cross the Pacific Ocean is 9 years at 80°N, 2 years at 15°N and only 1 year near the equator after Miyakoda's (1982) estimate. In equatorial regions, signals within the ocean propagate as Kelvin waves eastward with the speed of ~ 2m/s, and as Rossby waves westward with ~ 0.5m/s (Hurlbert et al., 1976; McCreary, 1976; Philander and Pacanowski, 1980). Because the equatorial ocean possesses such a relatively short time scale, the coupling between the atmosphere and ocean is of considerable interest and importance in the equatorial regions.

Lau (1981) constructed a very simplified coupled model in which the atmosphere is coupled with the ocean through thermal link and the ocean is coupled with the atmosphere through dynamical link. He simplified the model further to confine his study to the coupling between large-scale atmospheric and oceanic equatorial Kelvin waves only. He showed the existence of two time scales in his model. One of them (Mode I) is related to the atmospheric Kelvin wave and is mostly manifest in the atmospheric response. The other (Mode II) is related to the oceanic Kelvin wave and is the predominant mode in the equatorial climatic time-scale (see Fig.22). The time-scale and the amplitude of Mode II increases substantially with the increase of air-sea interaction. It is interesting to note that the numerical experiments of his simplified system show an El Niño-type oscillation in a baroclinic coupled system as a result of strengthening and subsequent weakening in the barotropic component of the wind.

Detailed coupled atmosphere-ocean circulation model was tried first by Manabe and Bryan (1969). They used a 1/3 sector model which is symmetric with respect to the equator and has a simplified square ocean. Later the coupled model was extended to the global model with a realistic geographical distribution of ocean without seasonal variation (Manabe et al., 1975; Bryan et al., 1979). Washington et al. (1980) also have reported a simulation study with a global realistic model with seasonal variatons. All these models consider the interaction process shown in Fig. 2.

Global distribution of sea surface temperature obtained by Manabe et al. (1979) is shown in Fig. 23. This shows success in simulating basic features of seasonal variation of SST. There are, however, important differences between the simulation and the actual features. For example, the amplitude of seasonal variation of zonal mean SST in mid-latitudes of northern hemisphere is too small. The model also gives too high SST along the periphery of the Antarctic continent. The effect of Peru current and upwelling along the equator is not simulated well. Therefore, a great deal of improvement is still needed for a fully realistic simulation of the coupled atmosphere-ocean system. The resolution of the oceanic model and the treatment of the cloud amount are considered to be among the central problems.

Figure 23. Global distribution of SST computed with the GFDL coupled atmosphere ocean circulation model for February and August. Observed ones are also shown for comparison. (Taken from Manabe *et al.*, 1979).



At present, it might be still too early for discussions about prediction of climatic fluctuations with the coupled atmosphere-ocean model, as no such attempts have yet been reported. However, many scientists in this field consider that the use of some kind of coupled atmosphere-ocean model is one of the most promising ways to extend the forecasting range of the climate fluctuations. We believe that comprehensive numerical models of the climate system have potentials to predict essentially all the potentially predictable climate signals. Such comprehensive models adequate for seasonal forecasting, however, would require predictive capability for soil moisture, snow cover and the large-scale diabatic processes within the atmosphere as well as the SST, especially in the tropics. There are also many other problems to be considered before such a numerical model approach could be justified. Establishment of procedures for near real-time retrieval of global SST, snow cover and soil moisture will be one of the most crucial ones.

REFERENCES

Angell, J.K. and J. Korshover. 1977. Estimate of the global change in temperature, surface to 100mb between 1958 and 1975. Mon.Wea.Rev. 105:375.

____________. 1978. Global temperature variation, surface to 100mb; an update into 1977. Mon.Wea.Rev. 106:755.

____________. 1981. Comparison of variations in atmospheric quantities with sea-surface temperature variations in the equatorial eastern Pacific. Mon.Wea.Rev. 109:230.

Arkin, P.A. 1982. The relation between interannual variability in the 200mb tropical wind field and the Southern Oscillation. Mon.Wea.Rev. 110:1393.

Barnett, T.P. 1981. Statistical prediction of North American air temperatures from Pacific predictors. Mon.Wea.Rev. 109:1021.

Bjerknes, J. 1966. A possible response of the atmospheric Hadley circulation to equatorial anomalies of ocean temperature. Tellus. 18:820.

____________. 1969. Atmospheric teleconnections from the equatorial Pacific. Mon.Wea.Rev. 97:163.

Bryan, K., S. Manabe and R.C. Pacanowski. 1975. A global ocean-atmosphere climate model. Part II. The oceanic circulation, J.Phys.Oceanogr. 5:30.

Charney, J.G. and J. Shukla. 1981. Predictability of monsoon in "Monsoon Dynamics" (Sir James Lighthill and R.P. Pearce eds.) Cambridge Univ. Press.

Chervin, R.M., W.M. Washington and S.H. Schneider. 1976. Testing the statistical significance of the response of the NCAR general circulation model to North Pacific Ocean surface temperature anomalies. J.Atmos.Sci. 33:413.

Chervin, R.M., J.E. Kutzbach, D.D. Houghton and R.G. Gallimore. 1980. Response of the NCAR general circulation model to prescribed changes in ocean surface temperature. Part II. Midlatitude and subtropical changes. J. Atmos.Sci. 37:308.

Davis, R.E. 1978. Predictability of sea level pressure anomalies over the North Pacific Ocean. J.Phys.Oceanogr. 8:233.

Dickinson, R.E. 1982. Feasibility of monthly and seasonal forecasting by numerical models. "Physical basis for climate prediction on seasonal, annual and decadal time scales". Leningrad, USSR, 13-17 September, 1982.

Fritz, S. 1982. Northern hemisphere 700mb heights and Pacific Ocean temperatures for winter Mon.Wea.Rev. 110:18.

Harnack, R.P. and H.E. Landsberg. 1978. Winter season temperature outlook by objective methods. J.Geophys.Res. 85:3601.

Harnack, R.P. 1979. A further assessment of winter temperature predictions using objective methods. Mon.Wea.Rev. 107:250.

____________. 1982. Objective winter temperature forecasts: An update and extension to the western United States. Mon.Wea.Rev. 110:287.

Horel, J.D. and T.M. Wallace. 1981. Planetary-scale atmospheric phenomena associated with the interannual variability of sea-surface temperature in the equatorial Pacific. Mon.Wea.Rev. 109:813.

Hoskins, B.J. and D.J. Karoly. 1981. The steady linear response of a spherical atmosphere to thermal and orographic forcing. J.Atmos.Sci. 38:1179.

Houghton, D.D. J.E. Kutzbach, M. McClintock and D. Suchman. 1974. Response of a general circulation model to a sea temperature perturbation, J.Atmos.Sci. 31:857.

Hurlbert, H.E., J.C. Kindel and J.J. O'Brien. 1976. A numerical simulation of the onset of El Niño. J.Phys.Oceanogr. 6:621.

Ichie, T. and J.R. Petersen. 1963. The anomalous rainfall of the 1957-58 winter in the equatorial central Pacific arid area. J.Meteor.Soc.Japan. 41:172.

Julian, P.R. and R.M. Chervin. 1978. A study of the Southern Oscillation and Walker Circulation phenomena. Mon.Wea.Rev. 106:1433.

Keshavamurty, R.N. 1982. Response of the atmosphere to sea surface temperature anomalies over the equatorial Pacific and the teleconnections of the Southern Oscillation. J.Atmos.Sci. 39:124.

Kutzbach, J.E., M. Clintock and D. Suchman. 1974. Response of a general circulation model to a sea temperature perturbation. J.Atmos.Sci. 31:857.

Kutzbatch, J.E., R.M. Chervin and D.D. Houghton. 1977. Response of NCAR general circulation to prescribed changes in ocean surface temperature. Part I: Mid-latitude changes. J.Atmos.Sci. 34:1200.

Lau, Ka-M. 1981. Oscillations in a simple equatorial climate system. J.Atmos.Sci. 38:248.

McCreary, J. 1976. Eastern tropical ocean response to changing wind systems with application to El Nino. J.Phys.Oceanogr. 6:632.

Manabe, S. and K. Bryan. 1969. Climate calculations with a combined ocean-atmosphere model. J.Atmos.Sci.26:786.

Manabe, S., K. Bryan and M.J. Spelman. 1975. A global ocean-atmosphere climate model. Part I. The atmospheric circulation. J.Phys.Oceanogr. 5:3.

____________. 1979. A global ocean-atmosphere climate model with seasonal variation for future studies of climate sensitivity. Dyn.Atmos.Oceans. 3:393.

Manabe, S. and D.G. Han. 1981. Simulation of atmospheric variability. Mon.Wea.Rev. 109:2260.

Miyakoda, K. 1982. Surface boundary forcings, "Physical basis for climate prediction on seasonal, annual and decadal time scales". Leningrad, USSR, 13-17 September 1982.

Miyakoda, K., T. Gordon, R. Caverly, W. Stern, J. Sirutis and W. Bourke. 1981. Simulation of a blocking event in January 1977. Preprints for Fifth conference on Numerical Weather Prediction, 2-6 November 1981. Monterey, CA, 99.

Moore, D.W. and S.G.H. Philander. 1977. Modeling of the tropical oceanic circulation. In The Sea, 6, Interscience, New York.

Moura, D.A. and J. Shukla. 1981. On the dynamics of droughts in northeast Brazil: observations, theory and numerical examples with a general circulation model. J.Atmos.Sci. 38:2653.

Namias, J. 1968. Long-range weather forecasting history, current status and outlook. Bull.Amer.Meteor.Soc. 49:438.

____________. 1969. Seasonal interactions between the Northern Pacific Ocean and the atmosphere during the 1960's. Mon.Wea.Rev. 97:173.

____________. 1971. The 1968-69 winter as an outgrowth of sea and air coupling during antecedent seasons. J.Phys.Oceanogr. 1:65.

____________. 1972. Experiments in objectively predicting some atmospheric and oceanic variables for the winter of 1971-72. J.Appl.Meteor. 11:1164.

___________. 1976. Negative ocean-air feedback systems over the North Pacific in the transition from warm to cold season. Mon.Wea.Rev. 104:1107.

___________. 1982. Case studies of long period air-sea interactions relating to long range forecasting. "Physical basis for climate prediction on seasonal, annual and decadal time scales". Leningrad, USSR. 13-17 September, 1982.

Namias, J. and R.M. Born. 1970. Temporal coherence in North Pacific Ocean and the atmosphere during the 1960's. Mon.Wea.Rev. 97:173.

Namias, J. and D.R. Cayan. 1981. Large-scale air-sea interactons and short-period climatic fluctuations. Science. 214:869.

Nap, J.L., H.M. Van den Dool and J. Oerlemans. 1981. A verification of monthly weather forecasts in the seventies. Mon.Wea.Rev. 109:306.

Newell, R.E. and B.C. Weare. 1976. Ocean temperatures and large scale atmospheric variations. Nature. 262-40.

Nicholls, N. 1980. Long-range weather forecasting: Value, status and prospects. Rev.Geophys.Space Phys. 18:771.

Oort, A.H. and T.H. Vonder Haar. 1976. On the observed annual cycle in the Ocean-atmosphere heat balance over the northern hemisphere. J.Phys.Oceanogr. 6:781.

Philander, S.G.H. and R.C. Pacanowski. 1980. The generation of equatorial of equatorial currents. J.Geophys.Res. 85:1123.

Rasmusson, E.G. and T.H. Carpenter. 1982. Variation in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Nino. Mon.Wea.Rev. 110:254.

Rogers, J.C. and H. van Loon. 1979. The seesaw in winter temperatures between Greenland and Northern Europe. Part II: Some oceanic and atmospheric effects in middle and high latitudes. Mon.Wea.Rev. 107:509.

___________. 1982. Spatial variability of sea level pressure and 500mb height anomalies over the southern hemisphere. Mon.Wea.Rev. 110:1375.

Rowntree, P.R. 1972. The influence of tropical East Pacific Ocean temperature on the atmosphere. Quart.J.Roy.Meteor.Soc. 98:290.

___________. 1976. Tropical forcing of atmospheric motions in a numerical model. Quart.J.Roy.Meteor.Soc. 102:583.

Shukla, J. 1975. Effects of Arabian Sea-surface temperature in Indian summer monsoon: A numerical experiment with GFDL mode. J.Atmos. Sci. 32:503.

___________. 1981. Dynamic predictability of monthly means. J.Atmos.Sci. 38:2547.

Shukla, J. and B.M. Misra. 1977. Relationships between sea surface temperature and wind speed over the central Arabian Sea and monsoon rainfall over India. Mon.Wea.Rev. 105:998.

Sirutis, J. and K. Miyakoda. 1981. Comparative integrations of global models with various parameterized processes of sub-grid scale vertical eddy transports. Preprints for Fifth conference on Numerical Weather Prediction. 2-6 November 1981. Monterey, CA 106.

Trenberth, K.E. 1976. Spatial and temporal variations of the Southern Oscillation. Quart.J.Roy.Meteor.Soc. 102:639.

van Loon. H. and R.A. Madden. 1981. The Southern Oscillation. Part I. Global associations with pressure and temperature in northern winter. Mon.Wea.Rev. 109:1150.

van Loon, H. and J.C. Rogers. 1981. The Southern Oscillation. Part II. Association with canges in the middle troposphere in the northern winter. Mon.Wea.Rev. 109:1163.

Wallace, J.M. and D.S. Gutzler. 1981. Teleconnections in the geopotential height field during the northern hemisphere winter. Mon.Wea.Rev. 109:784.

Walsh, J.E. and M.B. Richman. 1981. Seasonality in the associations between surface temperatures over the United States and the North Pacific Ocean. Mon.Wea.Rev. 109:767.

Washington, W.M., A.J.Semtner, Jr., G.A. Meehl, D.J. Knight and T.A. Mayer. 1980. A general circulation experiment with a coupled atmosphere, ocean and sea ice model. J.Phys.Oceanogr. 10:1887.

Weare, B.C. 1977. Empirical orthogonal analaysis of Atlantic Ocean surface temperature. Quart.J.Roy.Meteor.Soc. 103:467.

Weare, B.C. 1979. A statistical study of the relationships between ocean surface temperatures and the Indian monsoon. J.Atmos.Sci. 36:2279.

Weare, B.C., A.R. Navato, and R.E. Newell. 1976. Empirical orthogonal analysis of Pacific sea surface temperatures. J.Phys.Oceanogr. 6:671.

Webster, P.J. 1981. Mechanisms determining the atmospheric response to sea surface temperature anomalies. J.Atmos.Sci. 38:554.

____________. 1982. Seasonality in the local and remote atmospheric response to sea surface temperature anomalies. J.Atmos.Sci. 39:41.

Wright, P.B. 1979. A simple model for simulating regional short-term climatic changes. Mon.Wea.Rev. 107:1567.

Wyrtki, K. 1975. El Niño - the dynamic response of the equatorial Pacific Ocean to atmospheric forcing. J.Phys.Oceanogr. 5:572.

Yamamoto, R., T. Iwashima and M. Hoshiai. 1975. Change of the surface air temperature averaged over the northern hemisphere and large volcanic eruptions during the year 1951-1972. J. Meteor.Soc.Japan. 53:482.

Yamamoto, R. and M. Hoshiai. 1979. Recent change of the northern hemisphere mean surface air temperature estimated by optimum interpolation. Mon.Wea.Rev. 107:1239.

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

EL ROL DE LA TEMPERATURA SUPERFICIAL DEL MAR Y LA SUBSIDENCIA ATMOSFERICA EN LA DESCRIPCION DE LA ESTRUCTURA TERMICA DE LA CAPA DE INVERSION

Por

Pablo Lagos

Instituto Geofísico del Perú
Apartado 3747
Lima 100, PERU

Summary

Evidence is presented relating changing atmospheric temperatures with increasing altitude and climatic changes. These are in turn related to sea surface anomalies in the equatorial eastern Pacific.

The atmospheric inversion layer, i.e. thermal structure with altitude, changes seasonally, as does the mixed layer depth of the oceans. Great changes or anomalies in both have been related, indicating the air-sea phenomena are strongly driving the climate changes of South America's coastal, mountain and jungle systems.

INTRODUCCION

Recientemente se han observado cambios climatológicos en la costa central de Sudamérica relacionados con la ocurrencia del fenómeno de El Niño iniciado en Octubre de 1982, lo que ha motivado la ampliación de los estudios sobre el fenómeno de El Niño y las alteraciones climáticas realizadas hasta 1982 (Lagos, 1982). En este trabajo se presentan evidencias adicionales sobre los cambios climáticos observados durante El Niño 1972 y el Niño 1982-1983, basados principalmente en los datos de la temperatura atmosférica con altura, obtenidos en la estación de radio-vientos del Callao, Perú. Los resultados de este trabajo proporcionan mayor información sobre el rol que desempeñan las anomalías térmicas del mar, en los cambios climáticos en la Costa del Perú.

LA INTERACCION OCEANO-ATMOSFERA Y LAS FLUCTUACIONES CLIMATICAS

Namias (1965) planteó la hipótesis que las anomalías térmicas de gran escala en el mar podrían influir fuertemente en la atmósfera, particularmente en las variaciones climáticas de corto período y escala global. A partir de esta fecha han aparecido en la literatura científica numerosos estudios sobre la interacción océano-atmósfera. Estudios oceanográficos y metereológicos realizados recientemente han demostrado que las anomalías de la temperatura superficial del mar en el Pacífico central ecuatoriano juegan un papel muy importante en la circulación atmosférica y el clima (Donguy y Henin, 1980; Horel y Wallace, 1981; Rasmusson y Carpenter, 1982). Estudios de modelaje también han demostrado que las anomalías térmicas en el mar tienen una gran influencia en la circulación atmosférica (Webster, 1981; Hoskins y Karoly, 1981).

Experiencias del pasado y del presente nos permiten asociar la ocurrencia del fenómeno de El Niño con precipitaciones intensas y persistentes en el Ecuador y norte del Perú, así como con cambios bruscos en los recursos pesqueros a lo largo de la Costa Occidental de Sudamérica. Como el fenómeno de El Niño está identificado con la presencia de aguas anormalmente cálidas frente a las costas del Perú y el Ecuador, el efecto del océano en la atmósfera es evidente. Por otro lado, las alteraciones en la distribución de las precipitaciones son manifestaciones de los cambios climatológicos. Quinn y Neal (1983) han encontrado que, con períodos largos, en la región subtrópical de Chile las variaciones de la temperatura superficial del mar en la costa están relacionadas con las precipitaciones de igual período. En este trabajo se analizan los cambios producidos por las anomalías de la temperatura superficial del mar en los primeros dos mil metros de la atmósfera, región donde se presenta la capa de inversión térmica, en una escala espacial de aproximadamente dos mil kilómetros y escala temporal de semanas a varios años.

EL CLIMA EN LA COSTA Y LA CAPA DE INVERSION TERMICA

Por sus características topográficas el Perú posee una gran variedad de climas, los que pueden resumirse a tres tipos : a) áridos, templado y húmedo a lo largo de la Costa, b) frío y seco con lluvias estacionales a lo largo de la coordillera y los valles andinos y c) lluvioso, caliente y muy húmedo en la región selvática del Amazonas (fig. 1).

Existe una gran correlación entre las anomalías de la temperatura superficial del mar y las anomalías térmicas en la atmósfera a lo largo de la costa del Perú, pero no hay una correlación evidente con las anomalías térmicas atmosféricas en la región andina y la selva (Lagos, 1982).

En general, el clima a lo largo de gran parte de la costa peruana es de fresco a moderadamente caliente, húmedo y con el cielo cubierto por nubes bajas durante casi todo el año. La causa de este comportamiento climático se debe al efecto de la baja temperatura superficial del mar y a la subsidencia atmosférica. La baja temperatura del mar está asociada principalmente con los procesos de afloramiento costero y la subsidencia atmosférica está asociada con la circulación atmosférica en el Pacífico sudeste y la región ecuatorial. La subsidencia produce un calentamiento en la atmósfera, que sumado a la baja temperatura del mar da origen a la formación de una capa de inversión térmica en los primeros dos mil metros de la atmósfera, que persiste durante casi todo el tiempo, año tras año. Esta situación constituye una de las características más saltantes del clima en la costa peruana. La capa de inversión, como una característica permanente de la costa peruana, ha sido estudiada por primera vez por Prohaska (1973) usando los datos de la radiosonda de Lima para 1967. Igualmente Albrecht (1981) ha analizado datos similares para un período de 20 años.

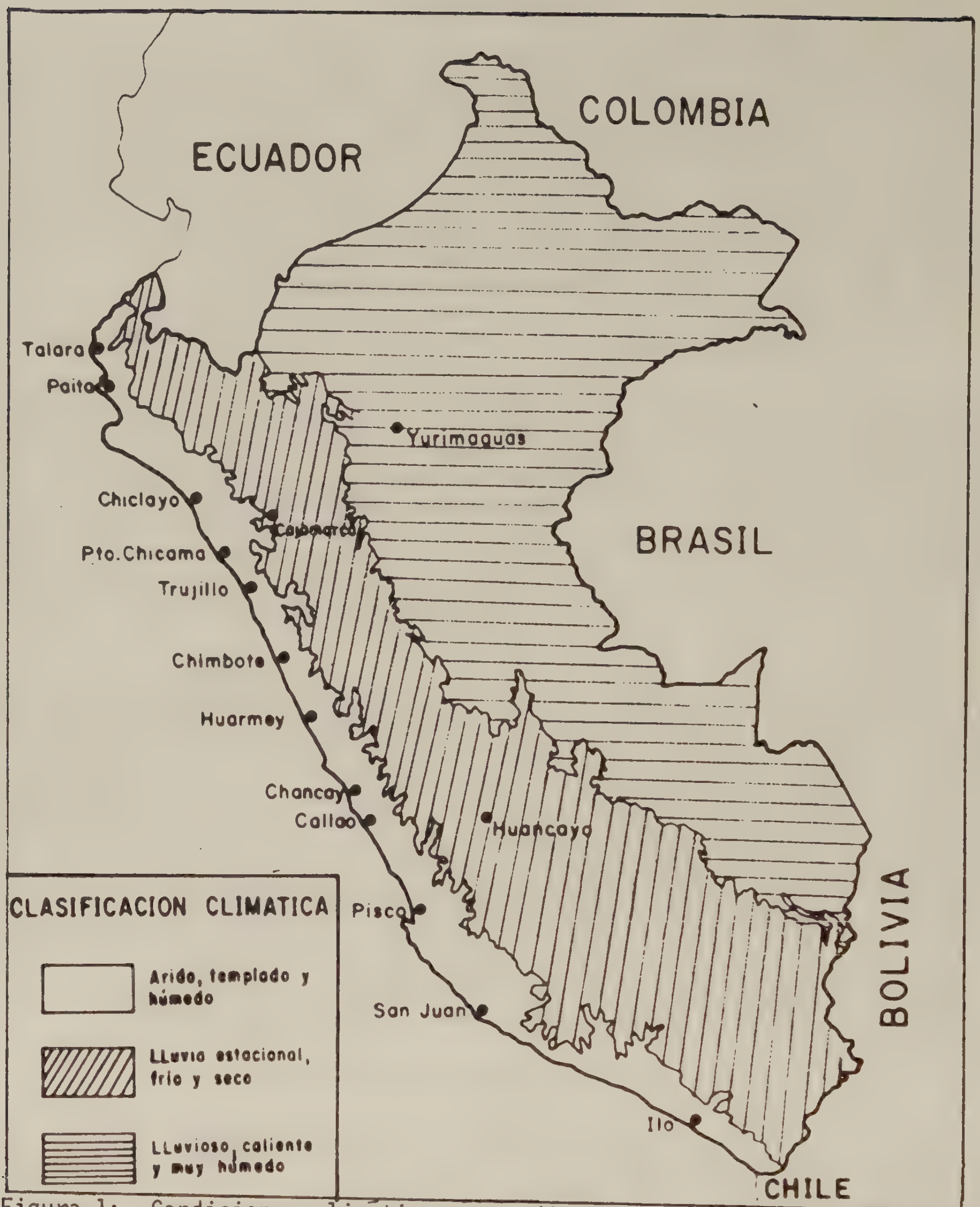

ECUADOR
COLOMBIA
BRASIL
BOLIVIA
CHILE
Talara
Paita
Yurimaguas
Chiclayo
Cajamarca
Pto. Chicama
Trujillo
Chimbote
Huarmey
Chancay
Callao
Huancayo
Pisco
San Juan
Ilo
CLASIFICACION CLIMATICA
Arido, templado y húmedo
LLuvia estacional, frio y seco
LLuvioso, caliente y muy húmedo

Figura 1: Condiciones climáticas promedios para la costa, la región andina y la selva en el Perú.

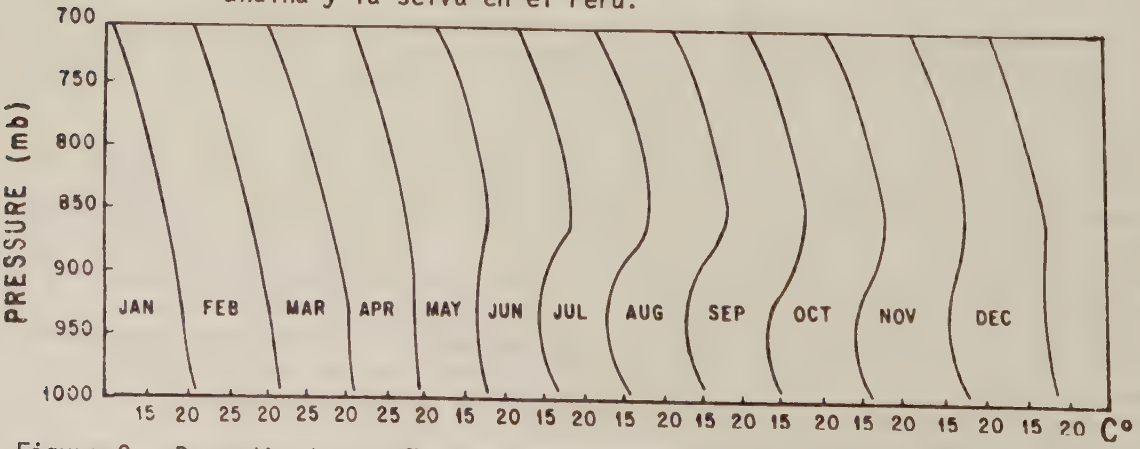


Figura 2: Promedio de 20 años de la estructura térmica mensual en la capa de inversión según Albrecht (1981).

La figura 2, muestra los promedios de 20 años de la estructura térmica en la capa de inversión obtenidos por Albrecht. Se puede notar que la inversión es más intensa y persistente durante los meses de invierno y débil durante los meses de verano.

Cuando la inversión térmica está presente en la atmósfera, se dice que la atmósfera es estable en esa región. En una atmósfera estable los procesos de convección vertical son nulos, permitiendo únicamente el desarrollo de una capa de nubes bajas del tipo stratus, en la capa de inversión. En estas condiciones es imposible la formación de cúmulus que permitirían desencadenar precipitaciones.

Durante la presencia de aguas anormalmente más caliente, asociadas principalmente con la ocurencia del fenómeno El Niño, la estructura térmica en la capa de inversión cambia notablemente. Cuando la temperatura superficial del mar alcanza los valores de 25°C, la capa de inversión se debilita completamente y la atmósfera en esta región se encuentra en una condición casi inestable.

Por otro lado, el calentamiento de la atmósfera por efecto de la subsidencia es también un factor que permite estabilizar o desestabiliazar la atmósfera en la capa de inversión, y es importante analizar el papel que desempeña cada uno de estos factores. Este análisis implica considerar principalmente la termodinámica de la capa de inversión.

BALANCE DE ENERGIAS EN LA CAPA DE INVERSION

Consideremos en forma simplificada la interacción océano-atmósfera en el dominio que incluye la capa superior del océano y la capa de inversión, es decir desde unos metros por debajo de la superficie del mar hasta una altura correspondiente a 700 mb de presión. El balance de energías en la capa de inversión se muestra en la figura 3. Nuestro interés es determinar el papel que juegan la temperatura del mar y el calentamiento por subsidencia en la estructura térmica de la capa de inversión. Para esto es necesario, en primera aproximación, resolver la ecuación de la termodinámica con condiciones de frontera escogidos apropiadamente. Todos los parámetros de esta ecuación a excepción de la velocidad vertical responsable de la subsidencia, se pueden medir o estimar con cierta exactitud, por tanto este último término puede ser estimado de la solución de la ecuación, y de esta manera se puede establecer su importancia.

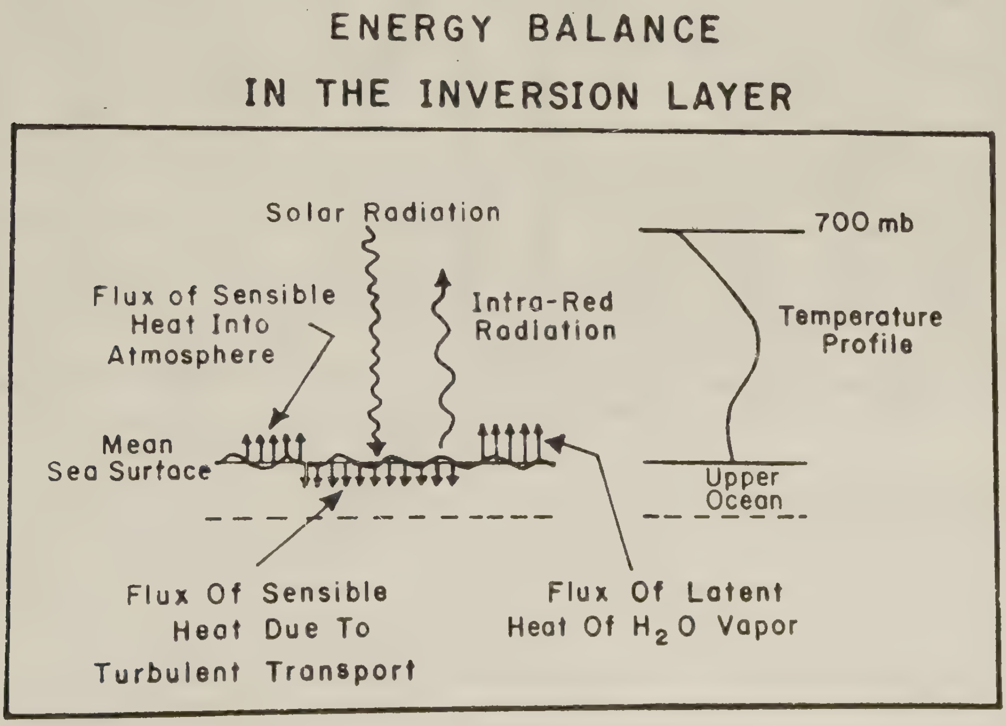


Figure 3: Balance de energías en la capa de inversión.

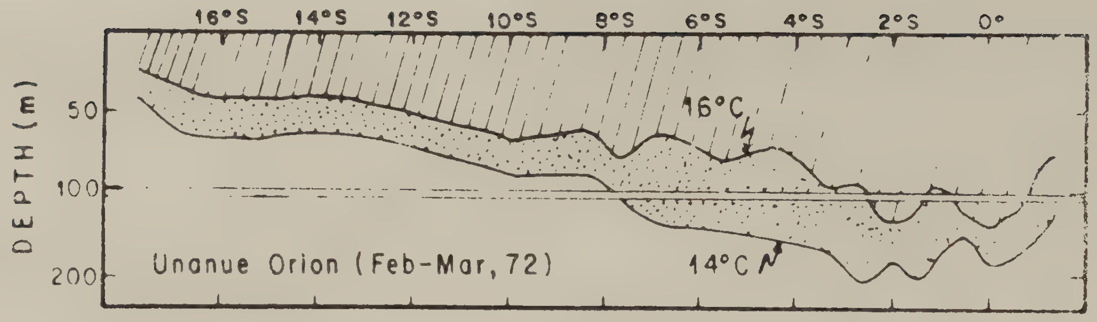


Figura 4: Sección vertical de la temperatura del mar (Febrero-Marzo, 1972), obtenidos con los barcos científicos Unanue y Orion.

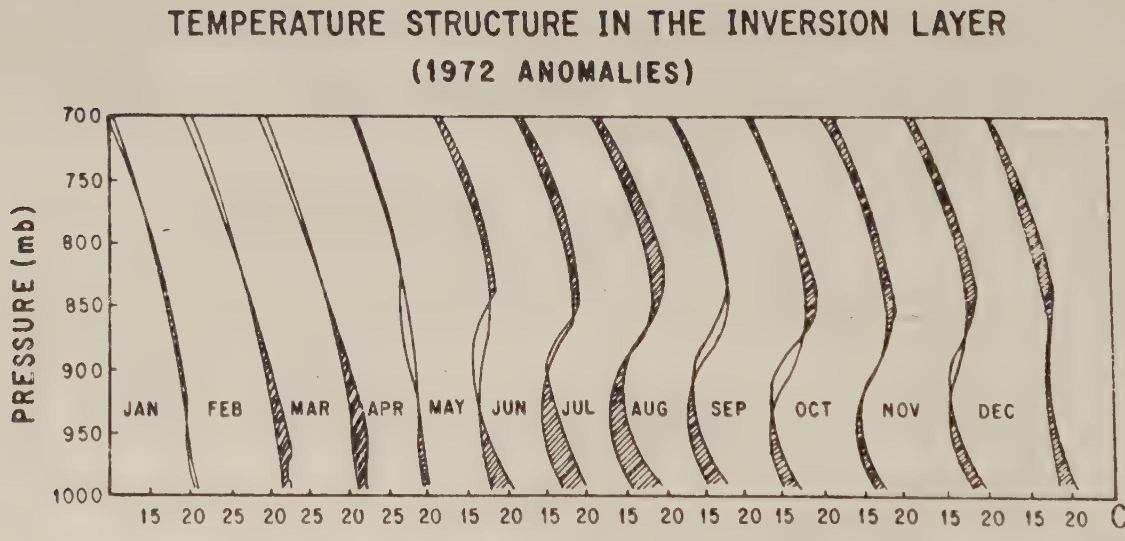


Figura 5: Anomalías mensuales de la estructura térmica en la capa de inversión para 1972

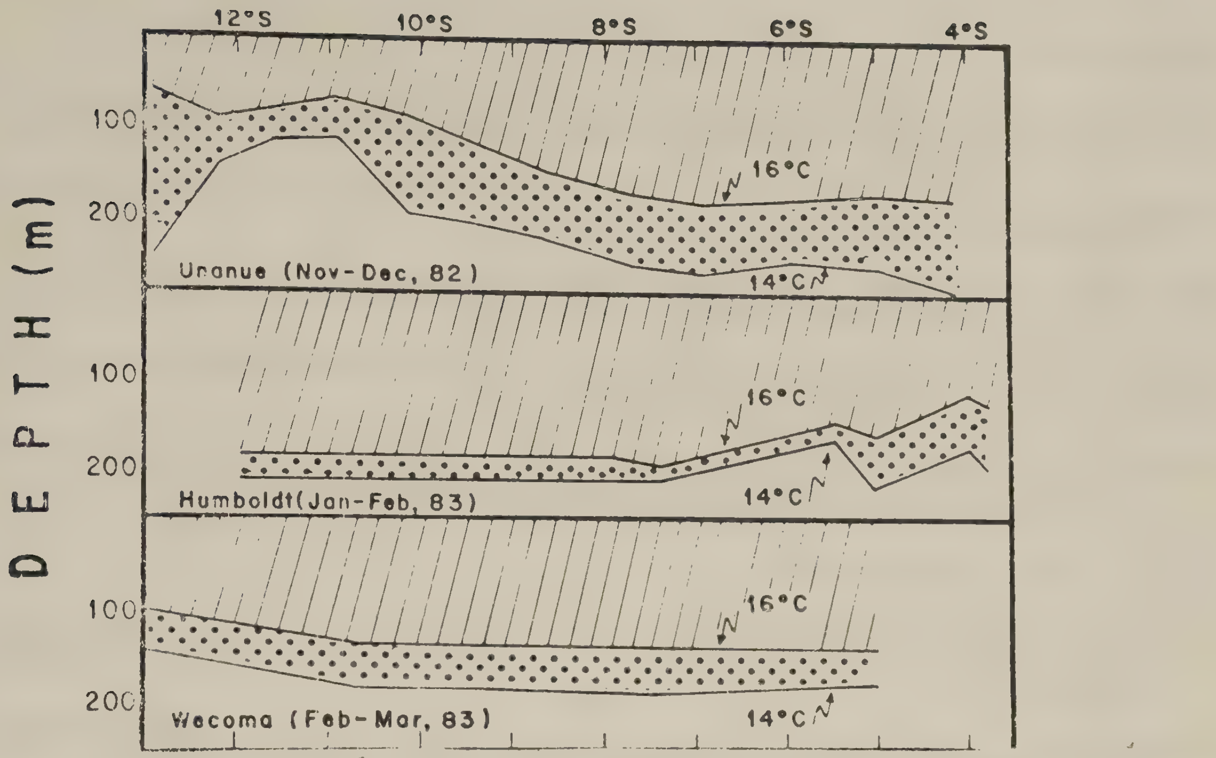


Figura 6: Sección vertical de la temperatura del mar (Noviembre-Diciembre 1982, Enero-Febrero 1983 y Febrero-Marzo 1983), obtenidos con los barcos científicos Unanue, Humboldt y Wecoma, respectivamente.

TEMPERATURE STRUCTURE IN THE INVERSION LAYER

(1982-1983 ANOMALIES)

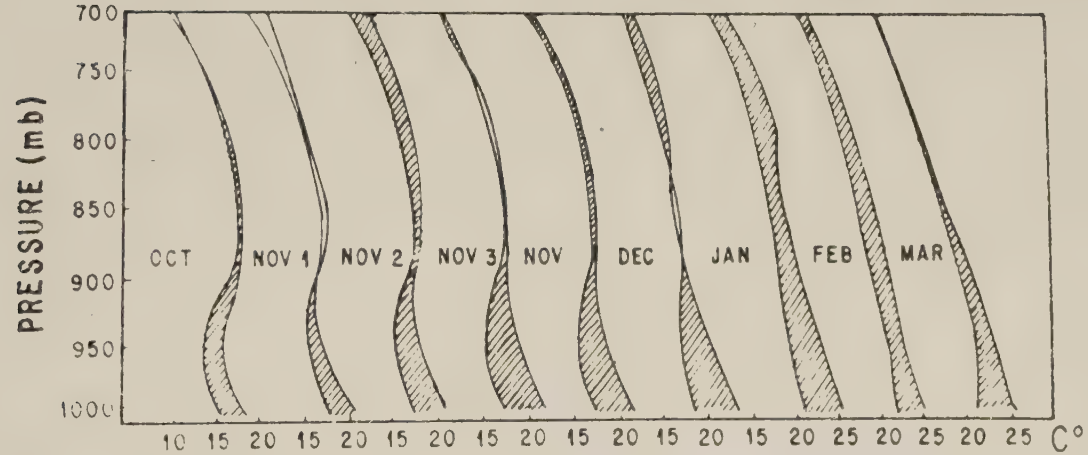


Figura 7: Anomalías de la estructura térmica en la capa de inversión para el período Octubre 1982-Marzo 1983.

Resulta interesante aplicar el análisis que se ha indicado en condiciones de grandes calentamientos del mar, tales como los ocurridos durante Los Niños de 1972 y 1982/1983. La figura 4 muestra la magnitud del calentamiento del mar a lo largo de la costa del Ecuador y Perú para el período de Febrero-Marzo de 1972. La figura 5 muestra la variación mensual de la estructura térmica en la capa de inversión para 1972. Las figuras 6 y 7 corresponden al período de Octubre 1982-Marzo 1983. En las figuras 5 y 7 las áreas sombreadas indican anomalías positivas. De estas dos figuras se puede deducir cualitativamente que el rol que juega la temperatura superficial del mar como factor desestabilizante de la atmósfera es más importante que el calentamiento por subsidencia. Los análisis cuantitativos que resulten de aplicar las sugerencias arriba indicadas se encuentran en progreso.

REFERENCIAS

Albrecht, J.A. 1981. The twenty year average atmospheric structure at Lima, Peru. Florida State University, Department of Meteorology, Tallahasee, June 1981.

Donguy, J.E. y C. Henin. 1980. Climatic teleconnections in western South Pacific with El Niño phenomenon. J.Phys.Oceanog. 10:1952-1958.

Horel, J.D. y J.M. Wallace. 1981. Planetary scale atmospheric phenomena associated with the southern oscillation. Monthly Weather Rev. 109:803-829.

Hoskins, B.J. y D.J. Karoly. 1981. The steady linear response of spherical atmosphere to thermal and orographic forcing. J.Atmospheric Sci. 38:1241-1259.

Lagos, P. (En prensa). Equatorial and Southeast Pacific experiments: present and future plans. Proceedings of the Study Conference on Large Scale Oceanographic Experiments in the World Climate Research Program. Tokyo, May 10-21 1982.

Namias, J. 1965. Science 147 :696.

Prohaska, F. 1973. Evidence on the climatic controls along the Peruvian coast. pp. 91-107. In Coastal deserts, their natural and human environments (Amira and Wilson, eds). University of Arizona Press.

Quinn, W.H. y V.T. Neal. (En prensa). Long-term variation in the southern oscillation. El Niño and Chilean Subtropical Rainfall Fishery Bulletin. 51, Nº2, 1983.

Rasmusson, E.M. y T.H. Carpenter. 1982. Variations in tropical sea-surface temperature and wind fields associated with the southern oscillation/El Niño. Monthly Weather Rev. 110:354-384.

Webster, P.J. 1981. Mechanism determining the atmospheric response to sea surface temperature anomalies. J.Atmospheric Sci. 38:554-571

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

CLIMATIC CHANGE:

PAST LESSONS AND FUTURE PROSPECTS

by

P.M. Kelly

Climatic Research Unit
School of Environmental Sciences
University of East Anglia
Norwich NR4 7TJ
United Kingdom

Resumen

En el presente trabajo se revisa el conocimiento actual relacionado con los cambios climáticos recientes. Se discute la disponibilidad de datos climáticos, los registros climáticos recientes, la representatividad de los datos, el uso adecuado de los métodos estadísticos, y la posibilidad de predecir el clima. Todo esto con la finalidad de proveer un esquema general de trabajo para los estudios de pesquería y el clima.

Hay una amplia discrepancia entre las escalas espaciales y temporales consideradas por los climatólogos y por los investigadores pesqueros, y se hacen algunas sugerencias sobre cómo reducir estas discrepancias.

INTRODUCTION

The aim of this paper is to outline current knowledge concerning recent climatic change in order to provide a broad framework for studies of fisheries and climate. Five major topics are discussed: the availability of climate data; the recent climatic record; data representativeness; the proper use of statistical methods; and the predictability of climate.

As will become apparent during the course of this discussion, there is a large discrepancy between the spatial and temporal scales considered by climatologists and fisheries scientists. While it is features of the microclimate that directly affect the fisheries resource, climatologists are, at present, preoccupied with macroclimatic variations on the hemispheric or global spatial scale, particularly in the area of climate prediction. This concentration is not a matter of choice. It reflects the current lack of detailed understanding of the physical processes underlying climatic change. If the impact on fisheries (and related socio-economic and political implications) of the long-term climate predictions discussed later are to be evaluated, this "scale gap" must be bridged. This is also necessary if the longer climatic records are to be used to determine historical impacts on fisheries. I make various suggestions as to how this might be achieved.

For the purposes of this paper, recent is defined as the last 100 years. A distinction is made between long-term climatic variations on time scales of 20 years and more, and shorter-term, interannual climatic variation.

DATA AVAILABILITY

The reliability of any scientific conclusion can be no greater than the quantity and quality of the data upon which it is based. Most studies of climatic change and its effects are hampered by limited data availability. Reliable instrumental climate data are only readily available for a few regions prior to the present century and, over much of the world, reasonable coverage is only available for the past four or five decades. A surprising amount of additional data exists in libraries and archives but has not yet been extracted and made available to the scientific community. With care, indirect or proxy climate information (based on historical, documentary evidence or biological indicators, for example) can be used to fill gaps in or to extend the instrumental record. A broad introduction to these techniques is given in Wigley et al. (1981). Use of such data may enable studies of the effects of climatic change on fisheries during historical times when the influence of socio-economic and political factors was, perhaps, less than today.

Although neglected by climatologists in comparison with other climatic parameters, there is a fair amount of data concerning variations in the atmospheric circulation. Gridded surface pressure data are available for much of the Northern Hemisphere for the post-1899 period. A similar data set, of much shorter duration, exists for the Southern Hemisphere. Upper air data, more indicative of the state of the atmospheric circulation but probably of less relevance to fisheries, are available for recent decades. Long records of wind speed, direction and frequency exist for various locations and some extend back two to three centuries. Lamb and Johnson (1966) have used lengthy station pressure records to derive indices of major features of the atmospheric circulation, back to 1750 in some cases. Principal component analysis provides a convenient means of efficiently extracting information from the large quantities of data in large-scale climate data sets. Applied to surface pressure data, it provides objective measures of the state of the atmospheric circulation. Kelly (unpublished) has used this method to identify characteristic patterns of change in the North Atlantic wind field. Interestingly, these patterns, tied to the major "centres of action" such as the Iceland Low, have a spatial scale of the order of hundreds of kilometers; much less than the large-scale nature of the data set would suggest. Analysing macroclimatic data in this way may facilitate correlation with microclimate-influenced fisheries.

Data concerning long-term variations in the climate of the oceans are extremely limited in availability, although recent compilations of marine data (sea-surface temperature, for example) have improved the situation somewhat. The worst gaps in the atmospheric data network are over the oceans. There is a need for more thorough documentation of past changes in the climate of the oceans and for better understanding of how atmospheric change affects the oceans (and vice versa).

All these data must be carefully checked for reliability. This is an exercise that is often neglected in climate studies. Even published or digitised data sets frequently contain inhomogeneities or errors (caused by mistyping or punching, instrument change, and so on). When searching for a weak signal in a noisy data set, data quality can seriously influence the chances of success. There are well-established methods of homogeneity-testing which should be routinely applied to a newly-acquired climate data set (see, for example, Salinger 1979). Moreover, the basic statistical characteristics of the data set should be examined. These may affect the performance of statistical techniques and/or tests applied to the data. Guidelines for correlation studies can be found in Pittock (1978), McCormac and Seliga (1979) and Kelly et al. (1982).

THE PAST 100 YEARS

The most reliable indicator of the state of the climatic system during the past 100 years is surface air temperature. While the coverage is, at present, restricted largely to the land masses, the record is more extensive in space and time than for any other climate variable and is reasonably well-tested and documented. Surface air temperature variations, particularly the large-scale averages presented here, are obviously a number of steps removed from the microclimatic factors affecting fisheries. Any attempt to link the variations described below with the vagaries of fisheries must trace these steps before cause and effect can be established with any certainty.

Surface air temperature averages are presented for three areas: the Northern Hemisphere, Arctic regions, and Antarctica. The derivation and limitations of these large-scale averages have been discussed by Jones et al. (1982), Kelly et al. (1982a) and Raper et al. (unpublished). As already mentioned, these data are largely for the land masses. Moreover, the spatial coverage decreases markedly in the late 19th century. The paucity of land and data limitations over the oceans preclude the calculation of a meaningful average for the Southern Hemisphere at this time.

The major climatic variation affecting the Northern Hemisphere during the post-1881 period was the warming of the early 20th century (Figure 1a). This may have begun early in the 19th century during the recovery from the "Little Ice Age", although the hemispheric record prior to 1881 remains to be established. The warming was strongest during the 1920's and 1930's, and culminated about 1940. Cooling occurred during the 1940's, 1950's and early 1960's, since which time warming has become re-established, whether or not this is a long-term phenomenon remains to be seen. The Northern Hemisphere record for the past 100 years is one of gradual warming, punctuated by episodes of cooling. The net warming over the period 1881 to 1982 is about 0.6^{o}C. There is some doubt as to the apparent coldness of the late 19th century. The spatial coverage of the data for the period may tend to over-estimate the trends inducing a spurious cooling of about 0.1^{o}C, but not enough to offset the overall warming trend. 1981 was the warmest year of the record and the most recent 10 to 15 years has been a time of great year to year variability.

Long-term trends have been similar in high northern latitudes (Figure 1b), but they have been greater in magnitude and have become apparent earlier. On shorter time scales, the hemispheric and Arctic variations have diverged at times. A recently compiled record of Antarctic temperature variations (Figure 2a) reveals marked warming (greater than in the recent Northern Hemisphere and Arctic records) during the past 20 to 25 years. The rate of warming is similar to that experienced over the Arctic during the 1920's and 1930's.

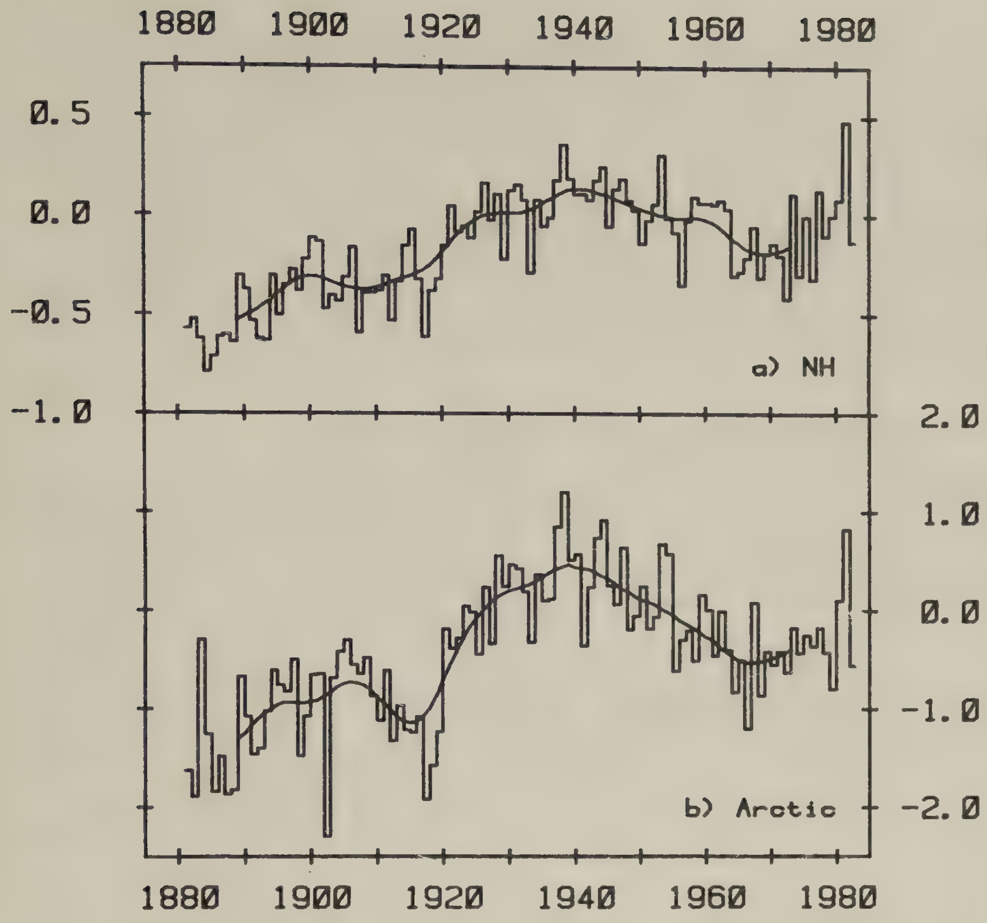


Fig. 1. Surface air temperature averages for a) the Northern Hemishpere and b) Arctic regions ($65-85^{o}N$). The data are annual averages expressed as departures in degrees Celsius from the 1946-1960 reference mean. They have also been filtered to reveal the long-term fluctuations.

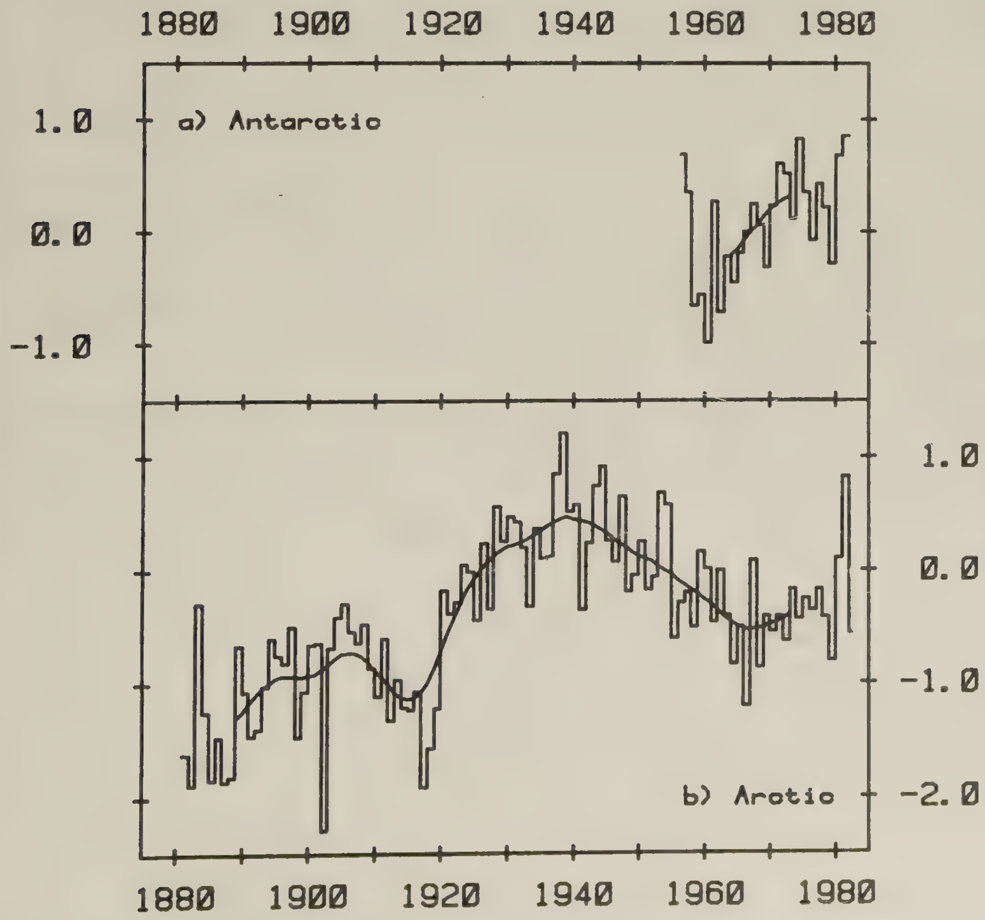


Fig. 2. Surface air temperature averages for a) Antarctica ($65-85^{o}S$) and b) Arctic regions ($65-85^{o}N$). The data are annual averages expressed as departures in degrees Celsius from the 1946-1960 reference mean. They have also been filtered to reveal the long-term variations.

These changes in surface air temperature were accompanied by fluctuations in other climatic parameters, by shifts in the atmospheric circulation (by variations in wind direction and strength and storminess, for example), and by variations in the ocean environment. These have been documented most thoroughly for the North Atlantic sector. Indeed, it is in this region that they appear to have been most marked. Cushing (1982) has recently summarized work on the fisheries impact of these events. The warming of the early 20th century was a large-scale phenomenon and there is much to be done in documenting the manifestations of this change on local spatial scales and in other aspects of the climate system. It appears to have been without parallel during the present millenium. Although warm episodes did occur during this time (Lamb, 1977), most appear to have been of shorter duration and/or lesser in spatial extent.

DATA REPRESENTATIVENESS AND STATISTICAL METHODS

The generalized account of global climatic trends in the preceding section provides a convenient summary of the major climatic variations of recent times. It must be realized, however, that the variations affecting a particular region may be different in magnitude, timing and, even, character. The Southern Oscillation, an essentially short-term variation, dominates these long-term trends in most equatorial regions. If large-scale averages are used in local or regional studies, their spatial representativeness needs to be carefully assessed. It is preferable to use local data whenever possible. Jones et al., (1982) have shown that the Northern Hemisphere temperature average is mostly indicative of conditions around the North Atlantic, sector. The only area that has varied consistently on long time scales with the hemispheric average is that of the Barents and Kara Seas. Similarly, seasonal representativeness has to be considered. When studing the impact of climatic change, it may well be that conditions at a particular time of the year are critical. Annual averages are frequently used in studies of climatic change, yet individual months may differ greatly in the trends that they exhibit. Long-term trends in surface air temperature have been greatest in April and May over the Northern Hemisphere as a whole (Jones et al., 1982). In Arctic regions, they have been strongest in January.

These points are illustrated in Figure 3. This record of annual and seasonal surface air temperature averaged over the eastern United States and the adjacent Gulf Stream shows a pronounced difference from the Northern Hemisphere curve shown in Figure 1a. Although slight warming is apparent in this area during the 20th century (most notably in autumn), the dominant long-term variation is a quasi-regular 20 to 25-year fluctuation. This is strongest in winter and hardly present in the autumn data. Kelly et al., (1982a) have documented the spatial and seasonal extent of this cycle which appears in both surface air temperature and pressure data for the area. Its occurrence in a region of strong thermal contrast between land, ocean and atmosphere suggests that its origin may lie in ocean-atmosphere interaction.

More generally, the selection of data is an important and often-neglected aspect of experiment design. There is a tendency for investigators to rely on inappropriate measures of the state of the climate system which have little relevance to the physical or biological processes to be studied.

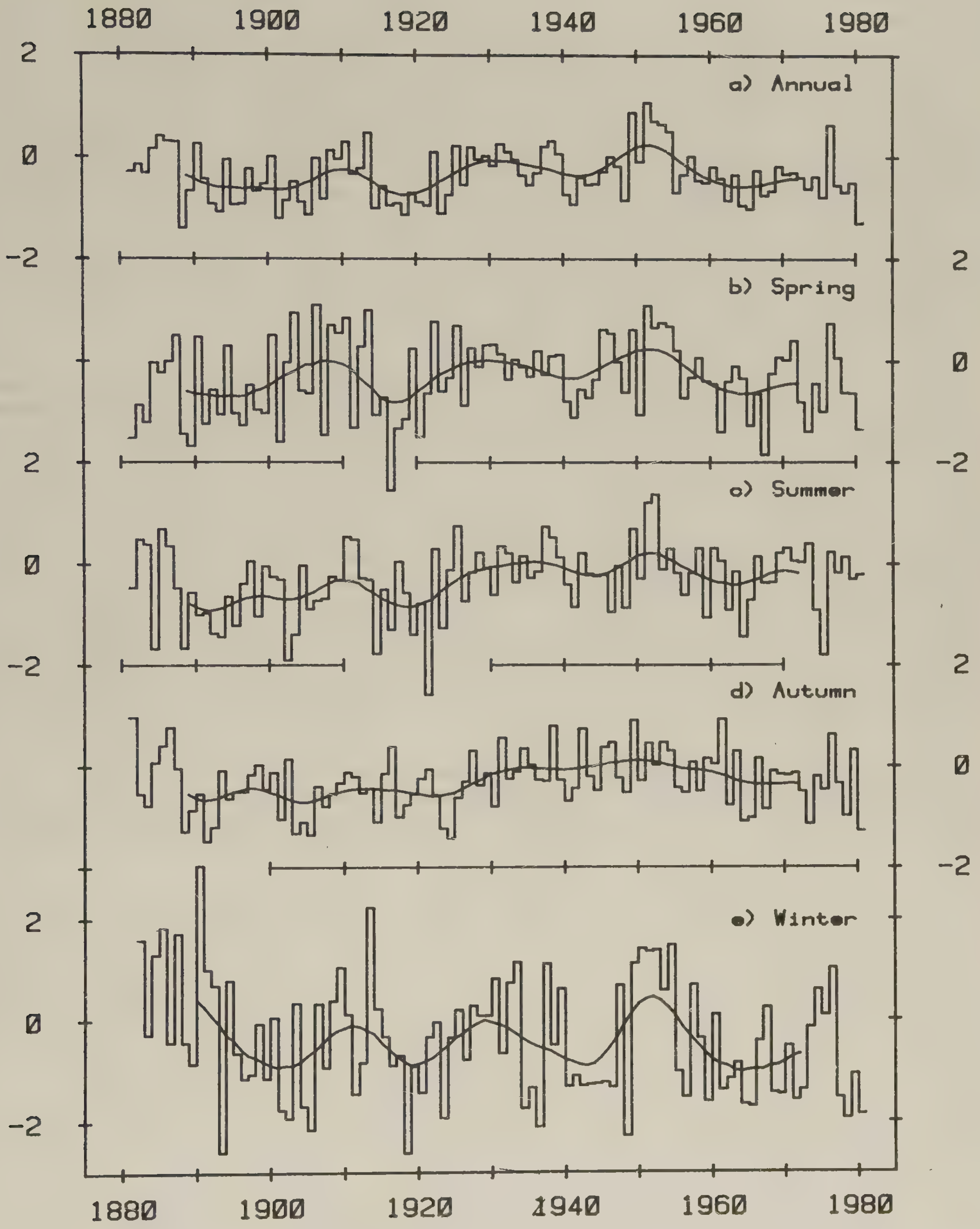


Fig. 3. Surface air temperature averaged over the eastern U.S. and the Gulf Stream region. Annual and seasonal data are presented as departures in degrees Celsius from the 1946-1960 reference mean. Seasons are defined in the standard manner (winter = DJF, and so on) and winters are dated by the year of the January. The data have been filtered to reveal the long-term variation.

STATISTICAL METHODS

There are many statistical techniques which can be used to identify the climate signal in fisheries data. The problem is to select the most appropriate method. The extraction of climate information from tree-growth measurements is an analogous area and I draw on my experience in that field in commenting on aspects of statistical practice and approaches. The problem of spatial scale has not, incidentally, proved a barrier to continental-scale climate reconstruction from regional grids of tree-ring data. The microclimatic factors directly influencing tree growth are related to some aspect of the large-scale climate field or atmospheric circulation (Fritts, 1982). Sophisticated semi-empirical techniques have been developed to identify this climate signal in tree-ring data (Hughes et al., 1982) and, although data-intensive, may be transferable to the field of fisheries-climate investigations.

In most cases, statistical rigour is easier to guarantee if the experiment is designed in terms of testing a particular hypothesis rather than as a "shotgun" correlation study. Again, the importance of consideration of underlying physical and biological processes is stressed. Exploratory data studies can be of value in suggesting likely physical or biological mechanisms but their results must be presented honestly: as hypotheses until tested on independent data. Similarly, the use of basically descriptive statistical methods to build semi-empirical models can be useful, particularly if supported by laboratory experiments or theoretical studies. Wherever possible, the reproducibility of statistical results (whether in the context of a hypothesis test or not) should be tested by repetition of the analysis on independent data. This is often the most certain test of significance. The implications of limited data availability must be taken seriously. It is unwise to attempt to develop or test a more sophisticated model than the available data (or degrees of freedom) warrant. Particularly in time series exhibiting strong trends, the effective number of degrees of freedom may be considerably less than the number of data points would suggest.

After such a list of caveats, it is, perhaps, worth noting that statistical rigour is a tool and not an end in itself. Valuable results can arise from studies in which statistical guidelines cannot be met. To be useful, however, they must be presented honestly, with their limitations admitted and their significance not over-stated.

THE FUTURE

Reliable climate prediction is dependent on adequate understanding of the causes of climatic change. This understanding is severely limited at the present time. While the principal factors influencing the climate system can be identified, their relative importance and the detailed physical processes underlying then remain unclear. Three likely causes of past and future climatic change are considered in this paper: one natural and two anthropogenic. Tokioka (this volume) discusses a fourth mechanism, ocean-atmosphere interaction, which is believed to be particularly important on the interannual time scale.

A complete review of the methods of short-term climate prediction is beyond the scope of this paper. Suffice it to say that most methods are essentially statistical in nature relying or empirical rules and/or parallels with previous times when the climate system was in a similar state. The most reliable approaches, such as those based on ocean-atmosphere interaction, have a firm basis in knowledge of the physical processes involved. The limit of reliable short-term climate prediction is, at this time, about six months. In certain circumstances, this may be extended to a couple of years (for example after a major volcanic eruption) but there is always the possibility that any such forecast may be invalidated by unforeseen events during the forecasting interval (such as another eruption!). The area of interannual climate prediction on time scales of one to ten years has been neglected although, arguably, it is in this area that the potential benefits are greatest. The remainder of this discussion concerns long-term prediction.

Much, but not all, of the long-term variation in Northern Hemisphere surface air temperature described earlier can be attributed to changes in the degree of explosive volcanic activity. There was only one major eruption during the period 1920 to 1950. Such eruptions "normally" occur about once every ten years. Major explosive eruptions inject large quantities of dust and gas into the upper atmosphere. This can remain for years producing a particulate and aerosol veil which alters the Earth's energy balance (and produces spectacular sunsets). The net result is warming in the upper atmosphere and cooling at the Earth's surface. A summary of empirical and theoretical research relating to the climatic impact of volcanoes has recently been published (Newell and Deepak, 1982). The eruption sequence of El Chichōn, Mexico, in spring 1982 is of particular interest in the context of fisheries studies. As well as producing a fine series of "Tequila Sunsets" during the second half of 1982, it may have accelerated and/or accentuated the dramatic swing in the Southern Oscillation and the El Niño that occurred that year. Warming in the upper atmosphere appears to have speeded up a change in the upper winds that was already underway, presaging the surface events. Surface cooling has affected the Northern Hemisphere during 1982, bringing temperatures down from the high of 1981 (Figure 1). Long-term predictions made during the 1960's and early 1970's often cited a resurgence in volcanic activity (following the lull of the early 20th century) as the basis for estimation of continued cooling in the future (but see Figure 1!)

The upswing in Northern Hemisphere temperature occurred about the time that the climatological community re-discovered earlier predictions of widespread warming owing to increasing levels of atmospheric carbon dioxide. The increase, caused by escalating consumption of fossil fuels and de-forestation, is well-established but the likely climate consequences are still a matter of some debate. Numerical models forecast a warming of 2 to 3°C by some time towards the middle of the 21st century. This is a climatic change of a magnitude and rapidity unmatched in post-glacial times. We have already experienced a Northern Hemisphere temperature rise of about 20% of the predicted amount during the past 100 years. This has had notable effects on the fisheries resource, inter alia, and the potential impact of a further 2°C rise over the next 70 years or so must be a cause of some concern. Is fisheries science able to predict the effects of such a change?

Clark (1982) contains reviews of much of the field of CO_2 - climate research (including societal impact studies) and includes discussion by Klein (1982) and others of attempts to model the past Northern Hemisphere temperature record.

The conclusions of these modelling efforts have been weakened by problems of data quality and statistical rigour but they suggest that a combined model with volcanic and carbon dioxide forcing explains most features of the recent climate record. It will, however, be some years before the current warming trend can be associated with increasing CO_2 levels with any confidence.

A POLEMIC

Any attempt at long-term prediction must take all possible influences on future climate into account. Assessing the net impact is difficult and, perhaps, impossible. Will an increase in the frequency of explosive volcanic activity offset CO_2-induced warming? Will internal mechanisms, such as ocean-atmosphere interaction, reduce or amplify the effects of increasing atmospheric CO_2? The uncertainties are great and can be used as an excuse for inaction. Yet, in my view, the potential consequences of a major climatic change over coming decades are too great for the issue to be sidestepped in this way. Particularly in the case of CO_2-induced warming, society has the means to avoid, avert or, at least, anticipate the worst impacts if it so chooses. How can sensible management or forward planning be achieved in the face of scientific uncertainty?

The Soviet Union has recently decided to implement the first stage of a sequence of large-scale water transfers from northern Arctic-flowing rivers south into European Russia, Kazakhstan and Central Asia (Kelly et al., in press). The need for this water is great. Current irrigation requirements in the south have nearly exhausted local water supplies and the lack of water is producing adverse environmental and ecological impacts. But the large-scale transfers themselves will have some adverse impacts. As well as local effects in the north, it is possible that the diversions will affect the Arctic ice cover and, hence, the climate of a much wider region (Micklin, 1981). The freshwater discharge produces a strong pycnocline in the Arctic Ocean and its marginal Siberian seas, inhibiting upward heat flow from the subsurface, from warmer Atlantic water, and maintaining the ice cover. Scientific knowledge is too limited to predict the net impact of the diversions but they are considered essential. Recognizing that adverse consequences are possible, the Soviet Union has adopted a flexible management policy for the transfers stressing the need for slow, stage-by-stage process with continual impact monitoring (Kelly _et_ _al_., in press).

I believe that in a situation where there are major scientific doubts but decisions must be made and progress or action achieved, these two interlinked concepts of flexibility (or diversity) and careful monitoring are one way forward; and not only in the field of climate and climate impact prediction.

REFERENCES

Clark, W.C. (ed.). 1982. Carbon dioxide review: 1982. Oxford University Press.

Cushing, D.H. 1982. Climate and fisheries. Academic Press, London.

Fritts, H.C. 1982. The climate-growth response. In Climate from tree rings (M.K. Hughes, P.M. Kelly, J.R. Pilcher and V.C. LaMarche Jr., eds). Cambridge University Press.

Hughes, M.K., P.M. Kelly, J.R. Pilcher and V.C. LaMarche Jr. (eds). 1982. Climate from tree rings. Cambridge University Press.

Jones, P.D., T.M.L. Wigley and P.M. Kelly. 1982. Variations in surface air temperatures: pt. 1. Northern Hemisphere, 1881-1980. Monthly Weather Review. 110:59 p.

Kelly, P.M. (Unpublished). Recent climatic variations in the North Atlantic sector. Paper presented at ICES Mini-Symposium on Climatic Variations in the North Atlantic and their Effects on Biota and Fisheries, Copenhagen, 13 October 1982.

Kelly, P.M., P.D. Jones, C.B. Sear, B.S.G. Cherry and R.K. Tavakol. 1982a. Variations in surface air temperatures. Pt. 2. Arctic regions, 1881-1980. Monthly Weather Review 110:71 p.

Kelly, P.M. T.M.L. Wigley and P.D. Jones. 1982b. Commentary on Detecting carbon dioxide effects on climate, by W.H. Klein. In Carbon dioxide reivew: 1982 (W.C. Clark, ed.). Oxford University Press.

Kelly, P.M., D.A. Campbell, P.P. Micklin and J.R. Tarrant. 1983. Large-scale water transfers in the USSR. Geojournal, in press.

Klein, W.H. 1982. Detecting carbon dioxide effects on climate. In Carbon dioxide review: 1982 (W.C. Clark, ed.). Oxford University Press.

Lamb, H.H. 1977. Climate, present, past and future. Volume 2: Climate history and the future. Methuen, London.

Lamb, H.H. and A.I. Johnson. 1966. Secular variations of the atmospheric circulation since 1750. Geophysical Memoirs, 110, Meteorological Office, London.

McCormac, B.M. and T.A. Seliga (eds). 1979. Solar-terrestrial influences on weather and climate. D. Reidel, Dordrecht.

Micklin, P.P. 1981. A preliminary systems analysis of impacts of proposed Soviet river diversions on Arctic sea ice. EOS. 62:489.

Pittock, A.B. 1978. A critical look at long-term sun-weather relationships. Reviews of Geophysics and Space Physics. 16:400.

Raper, S.C.B., T.M.L. Wigley, P.R. Mayes, P.D. Jones and M.J. Salinger. (Unpublished). Variations in surface air temperature: Pt. 3. The Antarctic, 1956-1981, submitted to Monthly Weather Review.

Salinger, M.J. 1979. New Zealand cimate: the temperature record, historical data and some agricultural implications. Climatic Change. 2:109.

Tokioka, T. (This volume). Influence of the ocean on the atmospheric global circulations and short-range climatic fluctuations.

Wigley, T.M.L., M.J. Ingram and G. Farmer (eds). 1981. Climate and history. Cambridge University Press.

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

CONDICIONES OCEANOGRAFICAS Y SUS FLUCTUACIONES EN EL PACIFICO SUR ORIENTAL

Por

Oscar Guillēn G.

Instituto del Mar del Perū
Apartado 22
Callao
Perū

Summary

The oceanographic conditions in the southeast Pacific are summarized and the characteristics of El Niño and Anti-El Niño periods are examined which show great changes in the physical, chemical and biological aspects.

The variability of the oceanographic conditions are inter-related with the biota, especially in the years: 1965, 1972 and 1976 when they had limiting effects on the productivity. Similarly examples are given of very cold years such as: 1964, 1968, 1970-71 and 1974-75 when particular effects on the productivity were observed.

INTRODUCCION

La Oceanografía del Pacífico Tropical Oriental ha sido descrita por Wyrtki (1964, 1965, 1966 y 1967). Stevenson et al. (1970) han confeccionado el Atlas de las Aguas Costaneras del Océano Pacífico en la América del Sur. Inostroza (1972) preparó el Atlas Oceanográfico para las Costas de Chile. Love (1970-77) ha publicado el Atlas Eastropac para el Pacífico Oriental. Bennett (1965) elaboró las cartas mensuales de salinidad para el Pacífico Tropical Oriental.

Frente a las costas de Chile las investigaciones oceanográficas han sido hechas por Gunther (1936), Wooster y Gilmartin (1961), Brandhorst (1963 y 1971), Robles (1966 y 1968), Brandhorst y Rojas (1967 y 1968), Brandhorst y Cañón (1967), Wooster (1970), Inostroza (1973), Silva (1973), Sievers y Silva (1973) y Robles et al. (1976).

Frente a las costas del Perú muchos estudios han sido hechos destacándose los realizados por Gunther (1936), Wooster (1952, 1960, 1961 y 1969), Posner (1957), Wooster y Cromwell (1958), Wooster y Gilmartin (1961), Wooster y Reid (1963), Wyrtki (1963, 1965, 1966 y 1967), Wooster et al. (1965), Guillén (1967, 1971, 1973 y 1976), Tsuchiya (1968), Cochrane y Zuta (1968), White (1969), Zuta y Guillén (1970), Stevenson et al. (1970), Smith (1971), Mujica (1972), Zuta y Urquizo (1972), Wooster y Guillén (1974) y Zuta et al. (1976).

La oceanografía de la región norte del frente ecuatorial ha sido descrita por Enfield (1976). Otros estudios han sido realizados por Austin (1958), Knauss (1960), White (1969), Stevenson y Taft (1970), Love (1970-77), Jones (1973) y Zuta et al. (1976).

El Panamá Bight ha sido estudiado por Wooster (1959), Forsbergh (1969), Stevenson (1970) y Stevenson et al. (1970). Asimismo, las condiciones oceanográficas en el Golfo de Panamá han sido resumidas por Schaefer et al. (1958) y Forsbergh (1963).

CONDICIONES OCEANOGRAFICAS EN EL PACIFICO SUR ORIENTAL

Temperatura

Wyrtki (1965) elaboró las cartas mensuales promedios de temperaturas en la superficie del mar (Fig. 1), las cuales muestran la presencia de una lengua caliente situada al oeste de las aguas afloradas frente a las costas del Perú y norte de Chile durante los meses de octubre a mayo.

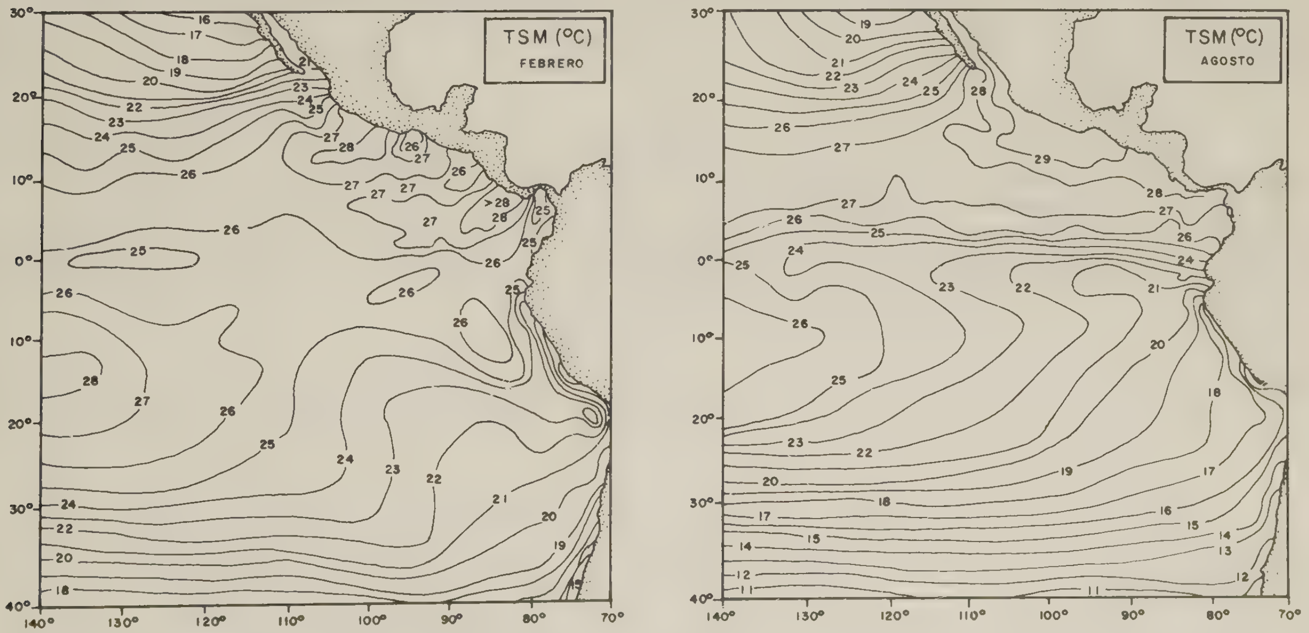


Fig. 1.- Temperatura promedio a 0m en febrero y agosto (de Wyrtki, 1964).

La distribución de la temperatura (Wooster, 1970) a lo largo de la costa es mostrada en la Fig. 2 en la que se observa los cambios estacionales bien marcados, las bajas temperaturas en el invierno y más caliente en el verano. El frente ecuatorial se encuentra al norte de los 5°S, donde corresponden los máximos gradientes de temperatura.

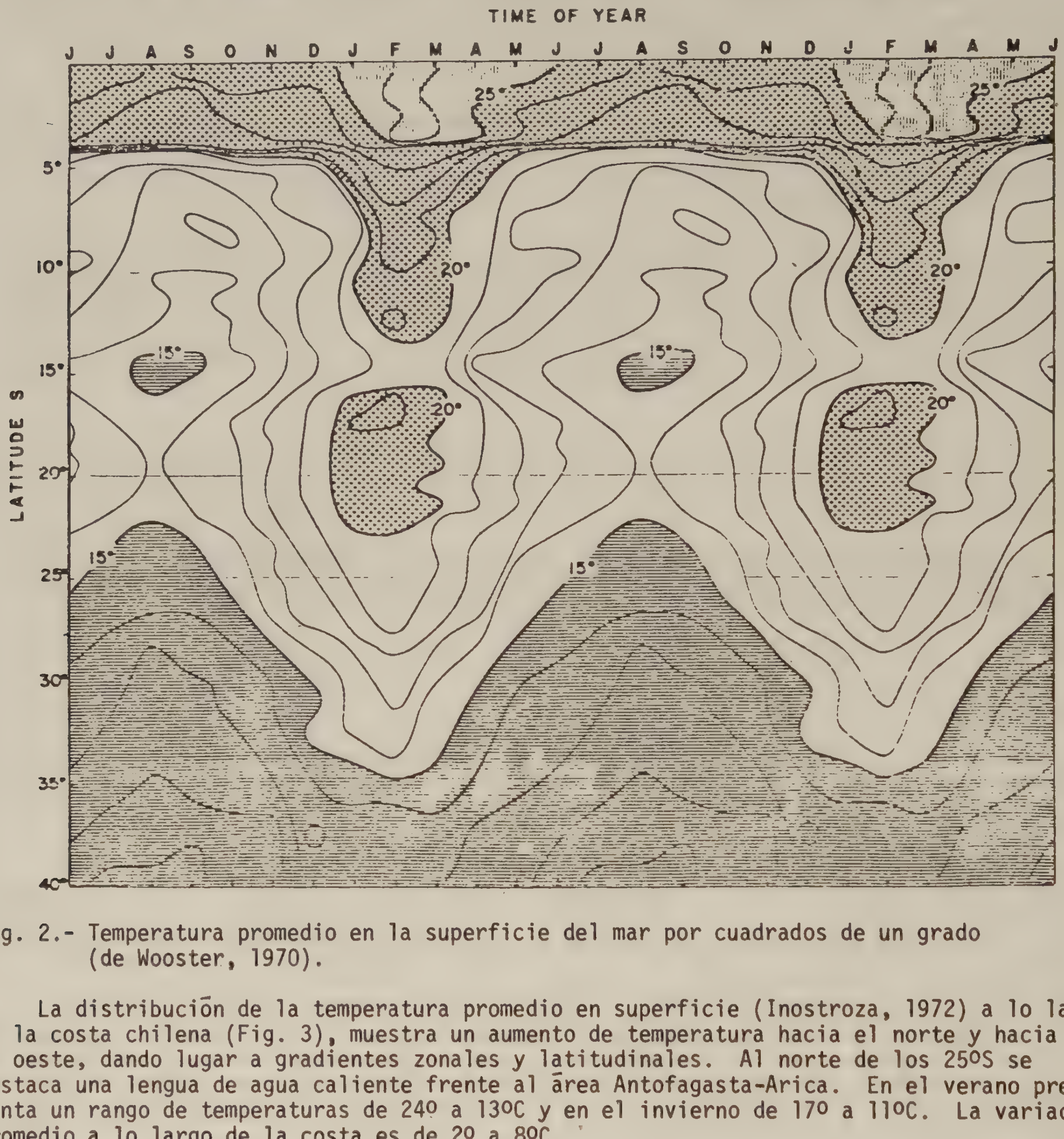


Fig. 2.- Temperatura promedio en la superficie del mar por cuadrados de un grado (de Wooster, 1970).

La distribución de la temperatura promedio en superficie (Inostroza, 1972) a lo largo de la costa chilena (Fig. 3), muestra un aumento de temperatura hacia el norte y hacia el oeste, dando lugar a gradientes zonales y latitudinales. Al norte de los 25°S se destaca una lengua de agua caliente frente al área Antofagasta-Arica. En el verano presenta un rango de temperaturas de 24° a 13°C y en el invierno de 17° a 11°C. La variación promedio a lo largo de la costa es de 2° a 8°C.

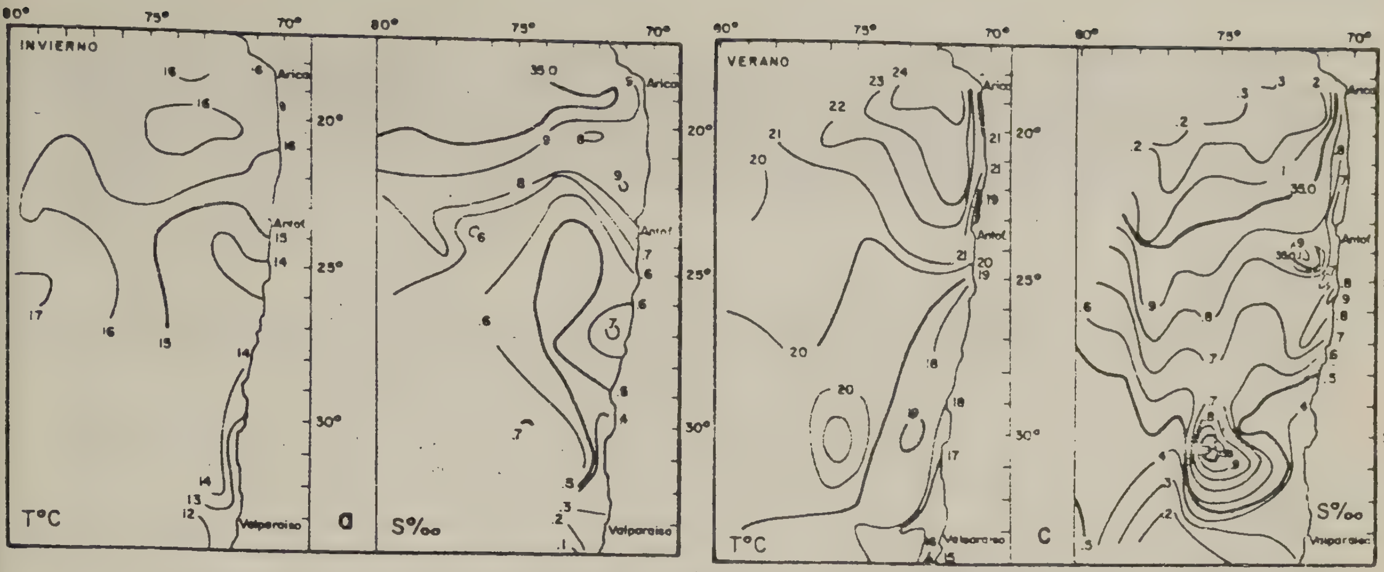


Fig. 3.- Temperatura y salinidad a Om en verano e invierno (de Inostroza, 1972)

Las temperaturas promedio en la superficie del mar (Zuta y Guillén, 1970; y Zuta y Urquizo, 1972) a lo largo de la costa peruana (Fig. 4) muestran un aumento de temperatura hacia el oeste y hacia el norte, dando lugar a gradientes zonales y latitudinales al sur y norte de los 6°S, respectivamente. Las temperaturas máximas se presentan en febrero-marzo, con un rango promedio de 17°-27°C y las temperaturas mínimas en agosto-septiembre con un rango promedio de 13° a 17°C. La variación anual promedio a lo largo de la costa peruana es de 5°-7°C. El área con temperatura más baja a lo largo del litoral peruano se halla situada entre los 14° y 16°S. Luego le siguen las áreas frías entre los 4°-6°S, 7°-9°S y 11°-13°S.

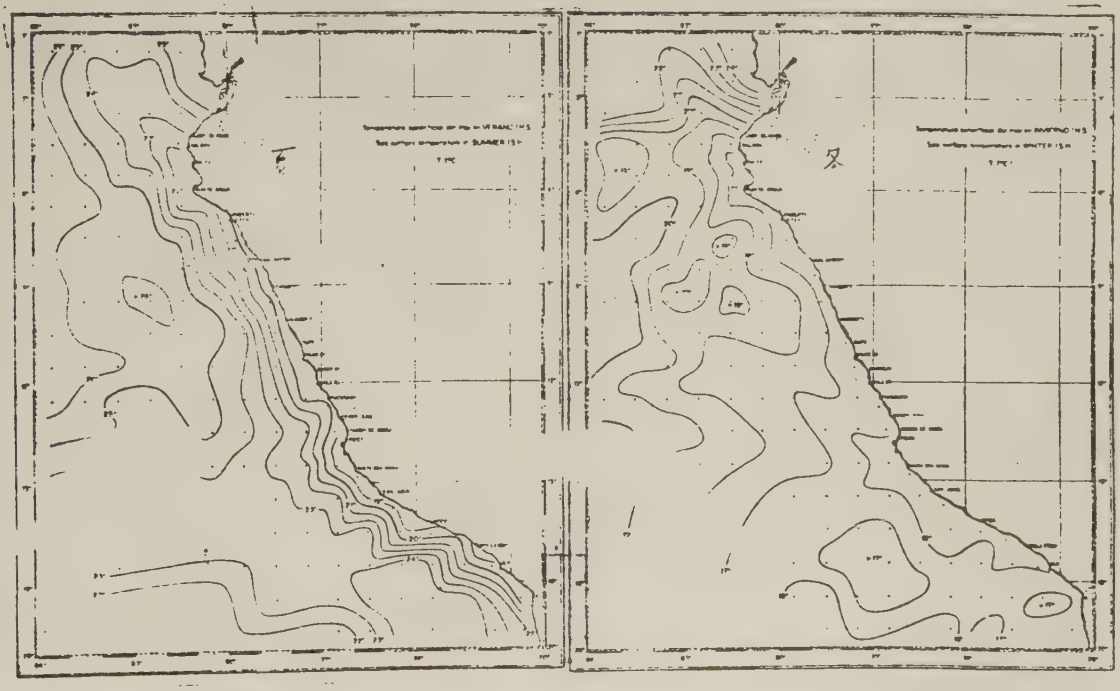


Fig. 4.- Temperatura promedio a Om en verano e invierno (de Zuta y Guillén, 1970).

Las temperaturas promedio frente al Ecuador, Colombia y Panamá (Enfield, 1976) presentan a lo largo de la costa un aumento de la temperatura hacia el norte, dando lugar a una zona de gradiente de temperatura o frente ecuatorial situado al norte de los 5°S. En invierno presenta una distribución casi zonal de temperatura máxima para las latitudes de 5°-8°N entre los meses de diciembre y abril y una distribución longitudinal de temperaturas mínimas para los meses de marzo y abril entre el Golfo de Panamá y 2°N.

Al sur de las Islas Galápagos se halla un área de baja temperatura debido a la surgencia ecuatorial, así como a la extensión hacia el oeste de la Corriente Peruana. Las variaciones de la temperatura son causadas principalmente por la variación estacional de la posición de la Zona de la Convergencia Intertropical(ZCIT) la cual puede hallarse frente a Panamá en el verano del hemisferio norte, o cerca al límite Colombia-Ecuador durante el invierno.

Salinidad

En el Pacífico Sudeste la salinidad máxima pasa de los 36.5 o/oo y la salinidad mínima se halla al noreste de las Galápagos con salinidades alrededor de 32 o/oo y frente a la costa meridional de Chile con salinidades alrededor de 33 o/oo.

La salinidad a lo largo de la costa (Inostroza, 1972) de Chile va aumentando hacia el norte (Fig. 3) desde valores de 33 o/oo a 40ºS a 35 o/oo al norte. La salinidad promedio al norte de los 34ºS es de 35.2 a 33.9 o/oo y de 35.0 a 33.8 o/oo en verano e invierno respectivamente. Al sur de los 37ºS se hallan los valores mínimos de salinidad (<34 o/oo). En el verano además se observa una lengua de agua salina (>35 o/oo) al norte de los 23ºS la cual se repliega en el invierno al norte de los 20ºS.

Frente a las costas del Perú (Zuta y Guillén, 1970) la salinidad en la superficie del mar (Fig. 5) presenta gradientes zonales al sur de los 6ºS, en donde la salinidad aumenta lejos de la costa. Al norte de los 6ºS presenta gradientes longitudinales pronunciados, debido al efecto de las Aguas Ecuatoriales Superficiales y Aguas Tropicales Superficiales. La salinidad en la parte netamente costera es de 35.1 a 34.8 o/oo. El rango promedio de salinidad en el verano e invierno es de 35.6 a 33.7 o/oo y de 35.5 a 32.0 o/oo, respec respectivamente.

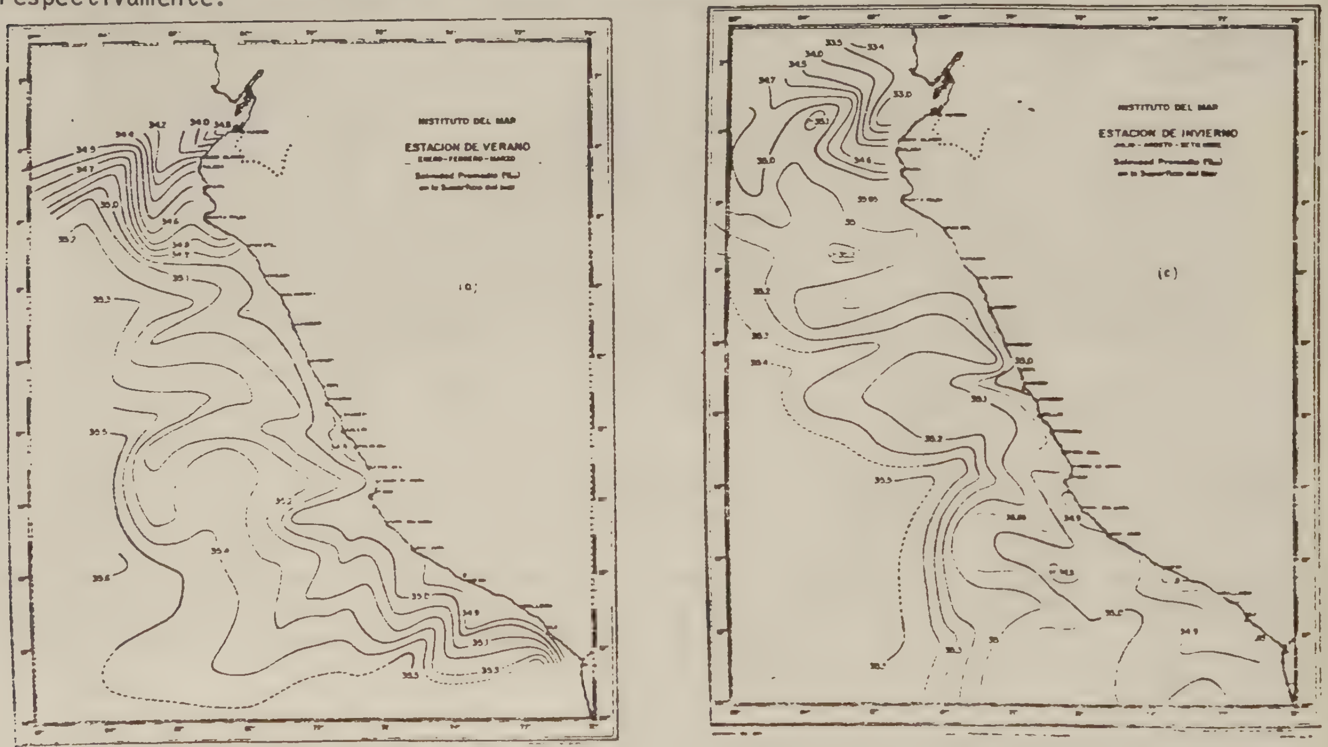


Fig. 5.- Salinidad promedio a 0m en verano e invierno (de Zuta y Guillén, 1970).

El rango de salinidades (Stevenson et al., 1970) a través del límite septentrional de la corriente del Perú varía estacionalmente y de año a año, hallándose los valores más altos de salinidad de julio a septiembre cuando la Corriente Peruana es más fuerte y los menores valores de enero a marzo, con valores de 33.5 a 35.0 o/oo, y 33.0 a 34.7 o/oo respectivamente.

Frente a las costas de Ecuador, Colombia y Panamá (Fig. 6) se encuentran las salinidades más bajas en los meses de octubre a diciembre, con los valores más bajos en noviembre, inferiores a 24 o/oo frente a Panamá Bight y salinidades menores de 33 o/oo a lo largo de la costa de Colombia y Ecuador hasta 1ºS. Las salinidades máximas se hallan en marzo y abril (mayor de 33 o/oo) en el Panamá Bight y (mayor de 34 o/oo) a lo largo de las costas de Colombia y Ecuador (Bennett, 1966). El mes de marzo quizás no es muy representativo para mostrar la distribución de la salinidad frente a la costa del Ecuador y sur de Colombia, ya que en este tiempo las lluvias son muy fuertes al norte del Ecuador y sur de Colombia debido al desplazamiento de la ZCIT hacia el sur. La celda de baja salinidad en la región de la Isla de Cocos se debe a un movimiento mar afuera de las aguas de baja salinidad provenientes del Panamá Bight.

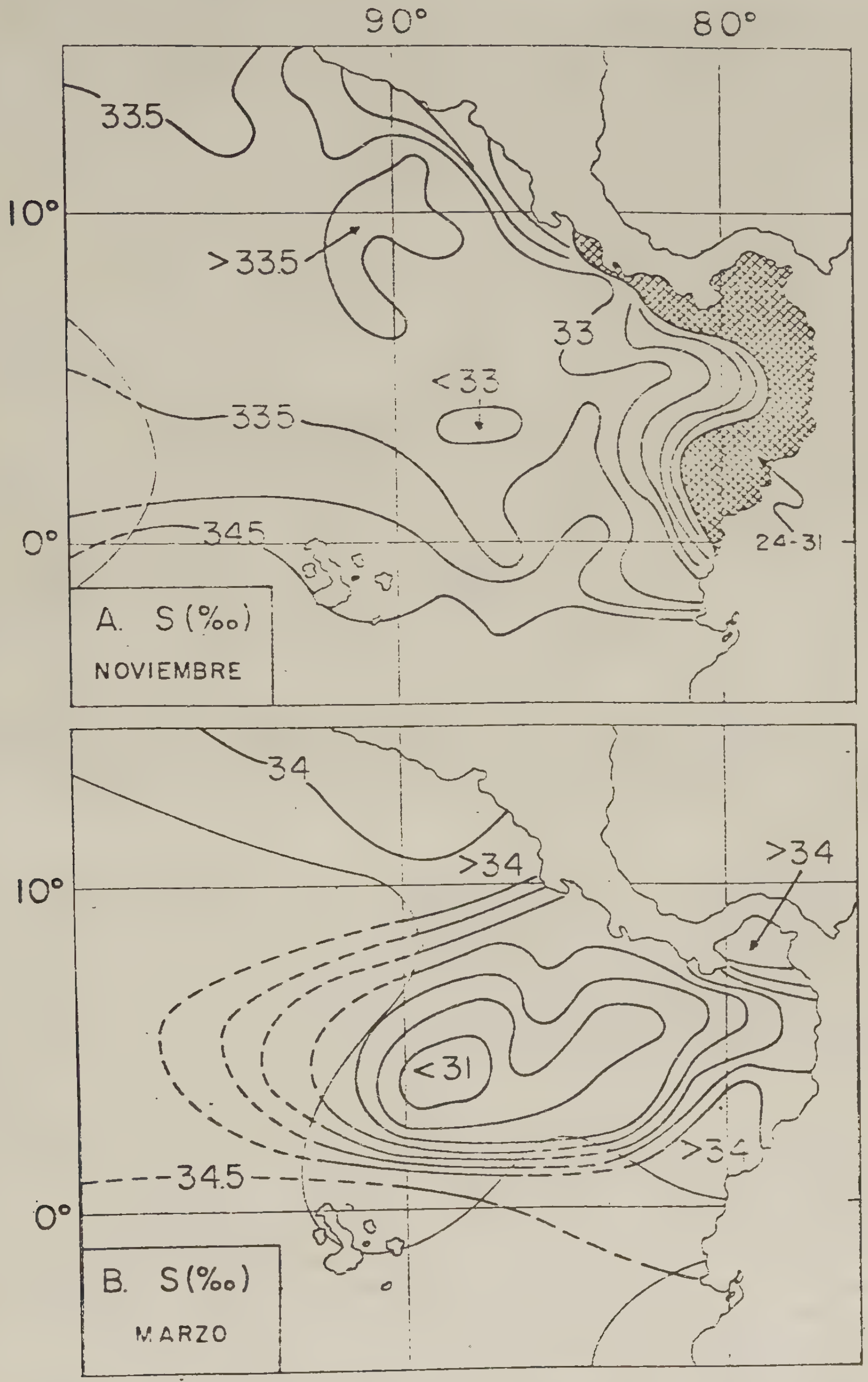


Fig. 6.- Salinidad promedio a 0m en marzo y noviembre (de Enfield, 1976).

La zona de convergencia intertropical se halla situada al norte del Panamá Bight de mayo a diciembre, cuando los vientos alisios SE son más fuertes, ocasionando intensas lluvias y descargas en el Bight. En esta época no hay afloramiento en el Golfo de Panamá, la corriente de Colombia es fuerte y el ramal occidental del remolino ciclónico que fluye hacia el sur del Bight es débil. En diciembre la zona de convergencia intertropical comienza a desplazarse hacia el sur.

Masas de Agua

Aguas Superficiales:

Wyrtki (1967) en la superficie del mar (Fig. 7) distingue las siguientes masas de aguas:

Aguas Tropicales Superficiales, que se caracterizan por su alta temperatura y baja salinidad y se presentan al norte de los 4°S, con salinidades menores de 34 o/oo y temperaturas mayores de 25°C. Las más bajas salinidades se hallan en el Golfo de Panamá y frente a las costas de Colombia, donde las salinidades varían de 34 o/oo a menos de 30 o/oo al final de la estación de lluvias (Bennett, 1965).

Aguas Subtropicales Superficiales, de alta salinidad y de un rango variable en temperatura (28° a 15°C) y con salinidades mayores de 35 o/oo, debido al exceso de la evaporación sobre la precipitación, salinidades mayores de 36 o/oo se hallan entre las latitudes 12°S y 25°S y longitudes 100°W y 150°W.

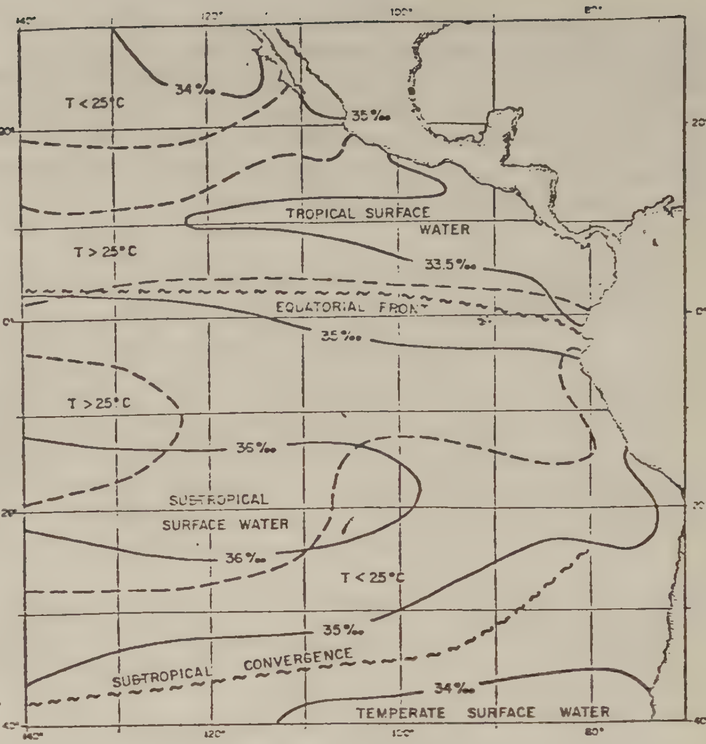


Fig. 7.- Principales masas de aguas superficiales en el Océano Pacífico Oriental: -Salinidad superficial, --- isoterma de 25°C: principales frentes oceánicos (de Wyrtki, 1966).

El límite norte de las Aguas Subtropicales Superficiales no coincide con el límite sur de las Aguas Tropicales Superficiales, excepto cerca a la costa del Ecuador. Entre estas dos masas de agua se encuentran las Aguas Ecuatoriales Superficiales, como producto de mezcla de dichas masas de aguas y se presenta generalmente al norte de los 6°S, con salinidades $<$34.8 o/oo (Zuta y Guillén, 1970).

El flujo hacia el norte de las aguas frías de la Corriente Peruana se opone a la tendencia natural de las Aguas Tropicales Superficiales que fluyen hacia el sur, dando como resultado la convergencia de las dos masas de agua y la formación del Frente Ecuatorial. Dicho frente ocupa una banda cuasizonal de cerca de 3° de latitud de ancho localizado entre los 0° y 5°S cerca del continente y se extiende en sentido oeste-noreste cerca de las Islas Galápagos, hallándose entre los 0° y 3°N. El frente se distingue con temperaturas desde 19° hasta 25°C y salinidades desde 35 o/oo a 33.5 o/oo de sur a norte, respectivamente.

Las aguas temperadas subantártidas del Pacífico Sur que fluyen hacia el este bajo la Corriente del Pacífico Sur, al aproximarse a la costa de Chile cerca de 50°S se dividen en dos brazos, uno hacia el sur y otro hacia el norte; este último fluye a lo largo de la costa de Sudamérica como parte del Sistema de Corrientes del Perú y Chile. Entre las latitudes 40°-50°S, la salinidad del agua superficial es reducida por las intensas lluvias y a la descarga de los ríos alcanzando valores menores de 33 o/oo. A medida que avanza hacia el norte su temperatura y salinidad incrementan lentamente alcanzando una salinidad superficial de 35 o/oo cerca de los 23°S.

Aguas Subsuperficiales:

Wyrtki (1967), ha realizado un estudio detallado sobre las masas de agua en la subsuperficie y señala que las Aguas Subtropicales Subsuperficiales y las de la capa mínima de oxígeno disuelto son las únicas formadas en la región. Las otras masas de agua son formadas fuera de la región y penetran dentro de ellas por medio del flujo horizontal y en gran escala debido a las mezclas horizontales.

Las Aguas Subtropicales, formadas en el medio del Pacífico Ecuatorial, se encuentran a lo largo del Ecuador como una lengua de máxima salinidad centrada aproximadamente entre los 100 m - 200 m de profundidad, las que son atrapadas por la Sub-corriente Ecuatorial (Corriente de Cromwell) y llevadas hacia el este. Cerca de las Islas Galápagos presenta un máximo cerrado de salinidad, el cual hace contraste con el agua subsuperficial menos salina del norte y sur del Ecuador (Stevenson y Taft, 1971).

La capa mínima de oxígeno disuelto frente al Perú se encuentra entre 15°C y 5°C, y tiene casi las mismas características de temperatura y salinidad señaladas por Sverdrup (1946)para la masa del Pacífico Ecuatorial. Esta misma agua fue llamada por Wyrtki (1963) Agua Ecuatorial Subsuperficial (Fig. 8). Frente al Perú, Zuta y Guillén (1970) hacen una diferencia denominando Aguas Ecuatoriales Subsuperficiales a las aguas asociadas con valores relativamente altos de salinidad (34.9 - 35.1 o/oo) y de oxígeno, vinculados a la extensión de la Corriente de Cromwell y Aguas Ecuatoriales Profundas a las aguas con salinidades de 34.9 - 34.0 o/oo y que coinciden con el mínimo de oxígeno y fluyen hacia el sur.

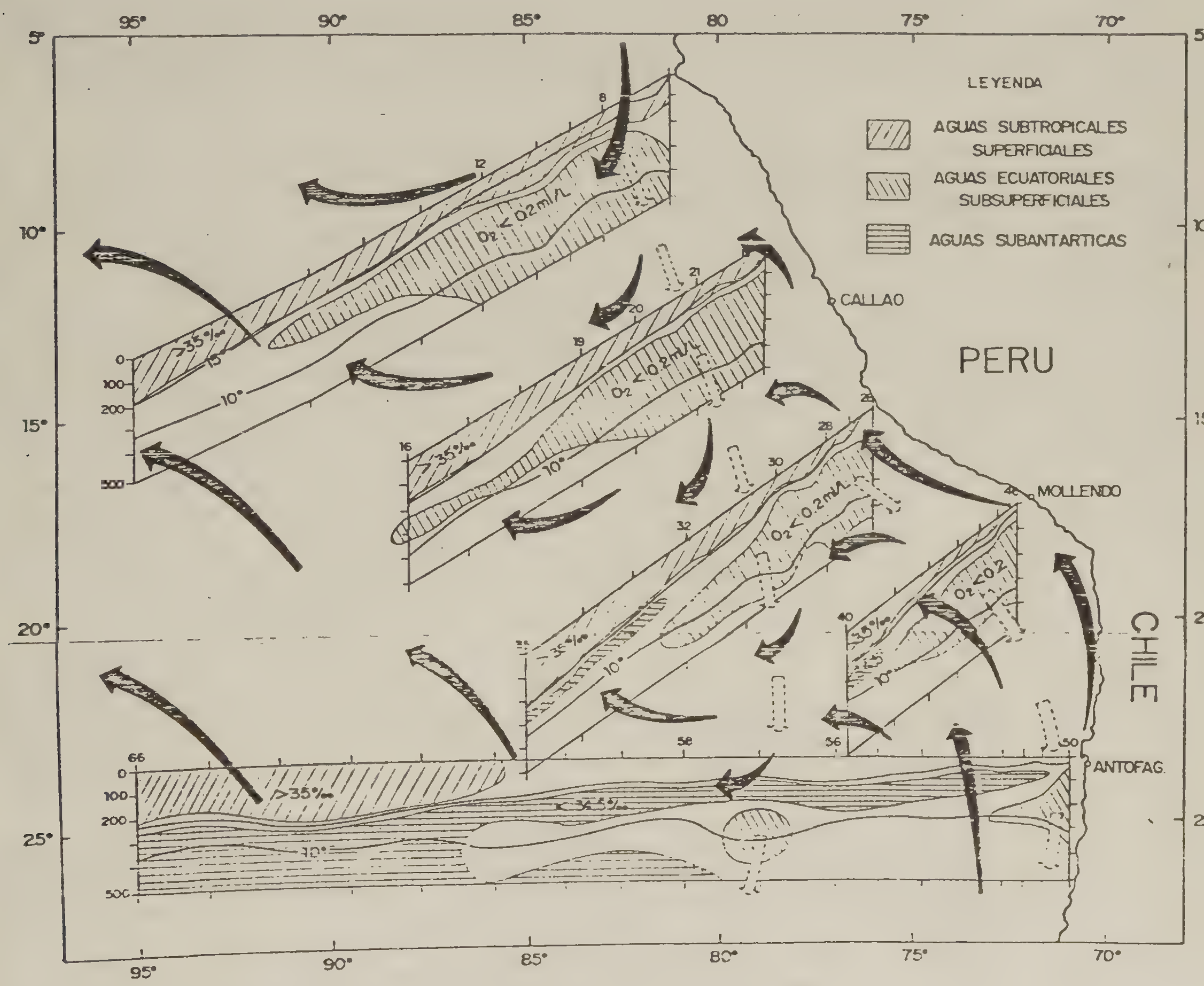

95°
90°
85°
80
75°
70°
5°
10°
15°
20°
25°
LEYENDA
AGUAS SUBTROPICALES SUPERFICIALES
AGUAS ECUATORIALES SUBSUPERFICIALES
AGUAS SUBANTARTICAS
CALLAO
PERU
MOLLENDO
CHILE
ANTOFAG.
>35‰
O2 <0.2ml/L
10°
0
100
200
500

Fig. 8.- Masas de agua frente al Perú y Chile (de Wyrtki, 1967).

La capa superior de las Aguas Ecuatoriales Subsuperficiales presenta dos máximos de salinidad con sus correspondientes mínimos de oxígeno: uno costero asociado a la Contracorriente Subsuperficial Peruano-Chilena, la cual avanza hasta más allá de 41°S (Robles, 1968; Alarcón y Pineda, 1969; y Wooster y Gilmartin, 1961), y otro oceánico más atenuado relacionado con la Contracorriente Oceánica Peruana descrita por Wyrtki (1963) y llega más allá de los 33°S.

Las aguas con salinidades menores de 34 o/oo y temperaturas menores de 15°C que fluyen hacia el norte de las costas de Chile cerca de la Convergencia Subtropical (Latitud 35°S) se hunden por debajo de las Aguas Subtropicales Superficiales que tienen salinidad y temperatura ligeramente mayor. Dicho flujo puede ser seguido por la salinidad mínima a 100 m de profundidad que se dirige hacia el norte de Chile y sur del Perú hasta cerca de los 15°S.

El Agua Antártica Intermedia se forma cerca del Frente Antártico Polar y se extiende hacia el norte entre las profundidades de 500 y 1500 m de profundidad (Wyrtki, 1967; y Robles, 1966) y se caracteriza por su mínima salinidad. Al sur de los 15°S la salinidad es menor de 34.5 o/oo y el contenido de oxígeno es alto. Al sur de 20°S la salinidad mínima coincide más o menos con la máxima de oxígeno (1.0 - 2.0 ml/L).

Circulación

Circulación superficial:

La circulación en la capa superficial en el Océano Pacífico (Fig. 9) está sometida al sistema de los vientos y a los movimientos giratorios anticiclónicos del Océano Pacífico del norte y del sur. Entre estos dos movimientos se encuentra la Contracorriente Ecuatorial.

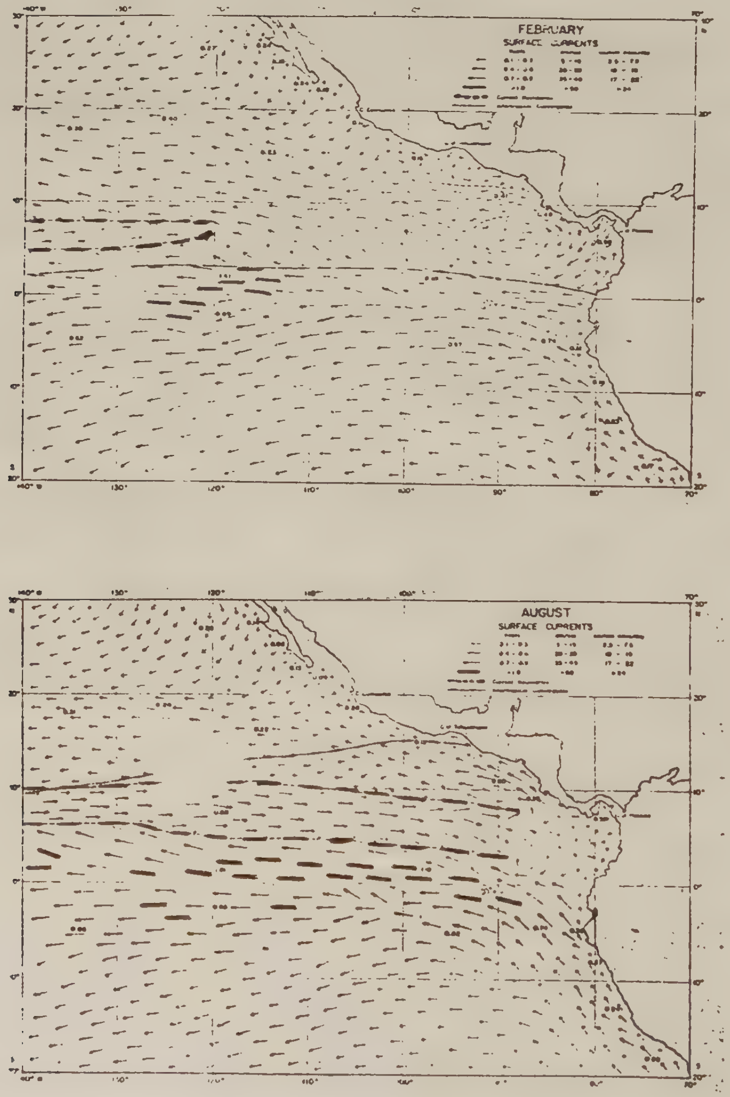


Fig. 9.- Corrientes superficiales en febrero y agosto (de Wyrtki, 1965).

Como parte de la circulación del Pacífico Sur las Aguas Subantárticas fluyen hacia el este alcanzando las costas de Chile entre las latitudes de 44° y 48°S y en el verano algo más hacia el sur; luego se dividen en dos ramales, uno que se dirige a lo largo de la costa hacia el sur, la Corriente de Cabo de Hornos; y la otra que se dirige hacia el norte, la Corriente de Humboldt o Chileno-Peruana, la cual tiene dos ramales, uno oceánico y otro costero. Frente a las costas de Chile, la rama oceánica es denominada Corriente de Chile (Wooster, 1970) o Corriente Oceánica Chileno-Peruana (Robles *et al.*, 1976), la cual fluye hacia el norte con velocidades de 12 cm/seg. Esta corriente transporta principalmente Aguas Subantárticas de relativamente baja temperatura y salinidad. La mayor parte de este flujo gira hacia el oeste antes de alcanzar los 20°S. La rama costera de la Corriente Chileno-Peruana es denominada Corriente Costera Chilena cuyo flujo es subantártico o netamente costero con velocidades de 25 cm/seg aproximadamente, y es observada a partir de los 28°S llegando algunas veces más allá de la Península de Mejillones en el invierno. Sievers y Silva (1976) dicen que la Contracorriente del Perú tiene presumiblemente dos ramas: la primera, oceánica, situada al oeste de los 77°W la cual avanza hasta los 27°S, coincidiendo con la ubicación dada por Wyrtki (1963). La segunda, costera, que avanza hacia el sur por los 75°W, extendiéndose hasta Valparaíso. Robles *et al.* (1976) señalan además una contracorriente que aparece inmediatamente hacia la costa, denominada Contracorriente Costera de Chile, que fluye hacia el sur alcanzando en el verano la latitud de 37°S, la cual está sujeta a variaciones estacionales alcanzando velocidades mayores de 15 cm/seg en el invierno.

Frente a la costa del Perú, la Corriente de Humboldt o Chileno-Peruana toma el nombre de Corriente Peruana conformada por la Corriente Costera Peruana y Corriente Oceánica Peruana, las cuales fluyen hacia el noroeste abandonando la costa cerca de los 5°S para luego integrarse en la Corriente Surecuatorial como parte de la circulación anticiclónica del Océano Pacífico Sur. Estas dos corrientes están generalmente separadas por un flujo débil e irregular hacia el sur, la Contracorriente del Perú, que es subsuperficial y ocasionalmente llega a la superficie del mar (Wyrtki, 1963). La Corriente Costera Peruana que es fría y rica en nutrientes tiene una velocidad promedio de 5 a 15 cm/seg, alcanzando algunas veces velocidades de 40 a 80 cm/seg cerca de los 7°S. Su flujo varía estacionalmente y es más intenso durante los meses de abril a septiembre, con un transporte confinado a los primeros 200 m de profundidad. La Corriente Oceánica Peruana es más intensa que la Corriente Costera Peruana y llega hasta los 700 m de profundidad. Presenta variaciones estacionales y durante los meses de julio a octubre forma un sólo flujo con la Corriente Costera Peruana hacia el oeste, integrándose luego en la Corriente Surecuatorial. La contracorriente en la superficie del mar es observada con mayor intensidad durante los meses de noviembre a febrero, estando ausente los meses de julio a octubre.

La Corriente Surecuatorial al oeste de las Islas Galápagos fluye hacia el oeste alcanzando las velocidades más altas en ambos lados del Ecuador, entre los 3°N y 8°S, aproximadamente. Su límite septentrional es la Contracorriente Ecuatorial cerca de los 4°N. Su velocidad promedio cambia poco durante el año al sur del Ecuador, mientras que al norte del Ecuador las velocidades son generalmente mayores y presentan una marcada variación estacional con velocidades mayores de 77 cm/seg de julio a noviembre.

La Contracorriente Ecuatorial (Wyrtki, 1965) al este de los 140°W, fluye hacia el este entre los 4° y los 11°N, cuya posición y anchura varía con la estación del año. De mayo a diciembre, la contracorriente se desarrolla claramente con una anchura que varía de los 3°-5° de latitud, logrando en septiembre las mayores velocidades. Al este de los 90°W la contracorriente se bifurca: una parte fluye hacia el norte y el noroeste alrededor del Domo de Costa Rica, y otra parte se dirige hacia el sur y al oeste ingresando en el sistema de la corriente sur ecuatorial. En enero la contracorriente comienza a dividirse y existe solamente en secciones separadas. En febrero y marzo, la contracorriente sólo llega hasta los 120°W para luego en abril desaparecer totalmente.

Frente al Panamá Bight la circulación superficial es en el sentido contrario a las agujas del reloj y presenta dos ramales; uno oriental, que fluye hacia el norte a lo largo de la costa denominada Corriente de Colombia (Wooster, 1959) y que a menudo penetra dentro del Golfo de Panamá, y otro Occidental, formado por el derrame de agua procedente de la entrada del golfo y que a menudo se une a la corriente sudeste que fluye a lo largo de la península panameña. En el invierno (Stevenson, 1970; y Stevenson *et al.*, 1970) del norte (febrero) el derrame superficial del Golfo de Panamá es más fuerte, alcanzando velocidades de 50 cm/seg. En esta época la Corriente de Colombia es estrecha y logra velocidades hasta de 150 cm/seg, mientras que en el Ecuador, época de lluvias, la circulación consiste de una serie de corrientes y de celdas que semejan remolinos, debido a la transición de la circulación del Panamá Bight a la del límite septentrional de la Corriente Peruana. En agosto la Corriente de Colombia, al norte de los 5°N, es más rápida que en las otras estaciones del año.

Circulación subsuperficial:

En la subsuperficie se tiene la Corriente Subsuperficial Peruano-Chilena, la Contracorriente Surecuatorial, la Subcorriente Ecuatorial y la Corriente de Chile.

La Subcorriente Ecuatorial (Knauss, 1960) fluye hacia el este desde por lo menos 140°W hasta 92°W, con velocidades máximas de 100 a 150 cm/seg con su núcleo cerca de la base de la termoclina, la cual asciende desde los 100 m de profundidad en el oeste hasta cerca de 40 m en el este. Su flujo hacia el este ha sido encontrado al este de las Islas Galápagos por Knauss (1966) y Stevenson y Taft (1971), y se considera que es una extensión de la Subcorriente Ecuatorial con velocidades observadas de 10 a 37 cm/seg, hallándose la corriente al norte y sur del Ecuador. White (1969) halló que la subcorriente se bifurca tanto hacia el norte como hacia el sur de las Galápagos, encontrándose el ramal sur entre los 2°S y 4°S a los 84°W.

La Corriente Subsuperficial Peruano-Chilena (Wooster y Gilmartin, 1961) nace de la unión de la extensión de la Corriente de Cromwell con la Contracorriente Surecuatorial (Cochrane y Zuta, 1968 ; y White, 1969) un poco al sur de los 6°S y lejos de la costa. Fluye hacia el sur próximo a las costas del Perú y Chile entre los 50 y 300 m de profundidad con velocidades de 4 a 10 cm/seg alcanzando 20 cm/seg frente a Punta Aguja. Su transporte y velocidad decrecen hacia el sur extendiéndose hasta cerca de los 40°S entre las profundidades de 100 y 300 m.

La Contracorriente del Perú fluye hacia el sur a lo largo de 80°W, principalmente, como una corriente subsuperficial llevando salinidad y bajo contenido de oxígeno entre los 100 y 500 m, siendo más fuerte cerca de los 100 m. Su transporte decrece hacia el sur de 10×10^{12} cm^3/seg en 5°S a 2×10^{12} cm^3/seg en los 22°S.

La Contracorriente Surecuatorial fluye de oeste a este entre los 8° y 10°S, aproximadamente entre los 100 y 500 m de profundidad con velocidades de 8 a 15 cm/seg, transportando 10 millones de m^3/seg. Esta contracorriente es más intensa entre julio y octubre y ha sido estudiada por Reid (1959 y 1961), Wooster (1961) y Wyrtki (1963).

La Corriente Chilena fluye hacia el norte y noroeste entre los 50 y 150 m de profundidad en la parte costera del Perú.

Afloramiento

A lo largo de la costa el afloramiento es muy superficial y está restringido principalmente a profundidades menores de 100 m. Frente al Perú las aguas de afloramiento se caracterizan por su baja temperatura, bajo contenido de oxígeno disuelto y alto contenido de nutrientes. La velocidad promedio del afloramiento frente a las costas del Perú es de 20×10^{-5} cm/seg con un rango de 5 a 30×10^{-5} cm/seg.

El afloramiento típico y casi permanente se presenta entre las latitudes 14°-16°S, luego le siguen las áreas 4°-6°S, 7°-9°S y 11°-13°S. Su intensidad varía de acuerdo a su posición geográfica y la estación del año, siendo más intenso en el invierno y mínima en el verano. Las aguas de afloramiento (Zuta y Guillén, 1970) a lo largo de la costa tienen tres orígenes: a) Las aguas de la extensión de la Corriente de Cromwell, las cuales afloran principalmente entre los 4°-6°S y que contribuyen en parte al afloramiento al norte de los 9°S; b) Las aguas de la Contracorriente Subsuperficial Peruano-Chilena que afloran principalmente al norte de los 12°S y que eventualmente en el verano y otoño pueden contribuir al afloramiento más hacia el sur; y c) Las aguas temperadas subantárticas, las cuales afloran principalmente al sur de los 14°S. El promedio del área de afloramiento es de 25 000 millas cuadradas.

Frente a las costas de Chile las áreas principales de afloramiento se hallan frente a 18º30'S (Arica), 19º30'S (Antofagasta), luego le siguen las áreas situadas entre los 23º y 29ºS. Al norte de Chile las temperaturas son bajas y las salinidades usualmente menores de 35 o/oo debido al afloramiento de las aguas temperadas subantárticas. Robles et al. (1976) hallaron un promedio de la profundidad de afloramiento del agua subantártica de 64 m y el promedio de la profundidad de afloramiento de las Aguas Ecuatoriales Subsuperficiales de 163 a 85 m.

En el Pacífico Ecuatorial Oriental las aguas superficiales más frías y la termoclina menos profunda son atribuidas a la divergencia superficial y al afloramiento bajo la influencia de los alisios SE. Lejos de la costa al sur de las Islas Galápagos se observa un área de baja temperatura, la cual refleja el afloramiento ecuatorial.

El afloramiento (Stevenson, 1970) se presenta más frecuentemente en el centro del Panamá Bight y a lo largo de la mitad del este de la entrada del golfo, ambos con velocidades de 45 x 10^{-4} cm/seg, siendo más intenso y fuerte durante febrero y marzo, aunque durante cada estación ocurren algunos afloramientos.

El Fenómeno El Niño

La designación de El Niño se aplica a las grandes anomalías oceánicas que ocurren de tiempo en tiempo frente a la costa de Sudamérica. El Fenómeno El Niño es ocasional, irregular, aperiódico y de grandes repercusiones socio-económicas para el Perú. Su origen no es bien conocido y parece estar ligado al debilitamiento general de la circulación de los vientos alisios del hemisferio sur.

El Fenómeno El Niño se presenta con diferentes intensidades con intervalos de 5 a 16 años y su duración es variable, presentando su mayor intensidad en los meses de febrero y marzo. Los eventos principales del fenómeno fueron los ocurridos en 1891, 1925-26, 1940-41, 1957-58, 1965, 1972-73, 1976 y 1982-83, los cuales alteraron temporalmente las condiciones del mar y del clima de la costa, con repercusiones enormes en la pesquería, la agricultura y el clima. Dentro de los últimos eventos secundarios del Fenómeno El Niño se hallan los ocurridos en 1953 y 1969.

Nutrientes y Oxígeno Disuelto

El oxígeno disuelto frente a las costas de Chile (Fig. 10) en la superficie del mar se halla con valores de 4.0 a 8.0 ml/L, predominando el rango de 5.0 a 6.0 ml/L (Forsbergh y Breenkow, 1965; Robles, 1966; e Inostroza, 1972).

Frente al Perú (Zuta y Guillén, 1970) la distribución superficial del oxígeno disuelto presenta valores promedio de 2.0-7.0 ml/L, correspondiendo los mínimos a las áreas de afloramiento. En el verano e invierno se hallan valores promedio de 7.0 a 2.0 ml/L, respectivamente.

El oxígeno disuelto en la superficie del mar frente a las costas del Ecuador, Colombia y Golfo de Panamá presentan valores promedio de 4.0 a 5.0 ml/L (Stevenson et al., 1970). Sin embargo, puede observarse algunas veces valores menores de 4.0 ml/L y mayores de 5.0 ml/L, debido a los procesos de afloramiento y fotosíntesis, respectivamente. Parra (1977) halló valores en la superficie del mar de 2.5 a 6.7 ml/L de oxígeno disuelto.

Las concentraciones de nutrientes en la capa superficial decrecen debido a su utilización por el fitoplancton y son abastecidas por la descomposición de la materia orgánica in situ y por los procesos de afloramiento, los cuales abastecen de nutrientes a las aguas superficiales. Entre los nutrientes tenemos: los fosfatos, silicatos y nitratros.

Frente a las costas de Chile (Fig. 10) los nutrientes presentan valores bajos en la superficie del mar en comparación con las costas del Perú. Los fosfatos a lo largo de la costa presentan un rango promedio de 2.0 a 0.25 ug-at/L (Reid, 1962; Forsbergh y Broenkow, 1965; e Inostroza, 1972), correspondiendo los mayores valores a las áreas cerca de la costa. En la superficie a la latitud 23ºS se observaron concentraciones menores de 1.0 ug-at/L, 5.0 ug-at/L y 10 ug-at/L de fosfatos, nitratos y silicatos, respectivamente; y a la latitud 33ºS se hallaron valores menores de 0.4 ug-at/L de fosfatos y 1.0 ug-at/L y 5.0 ug-at/L de silicatos y nitratos, respectivamente (Forsbergh y Broenkow, 1965).

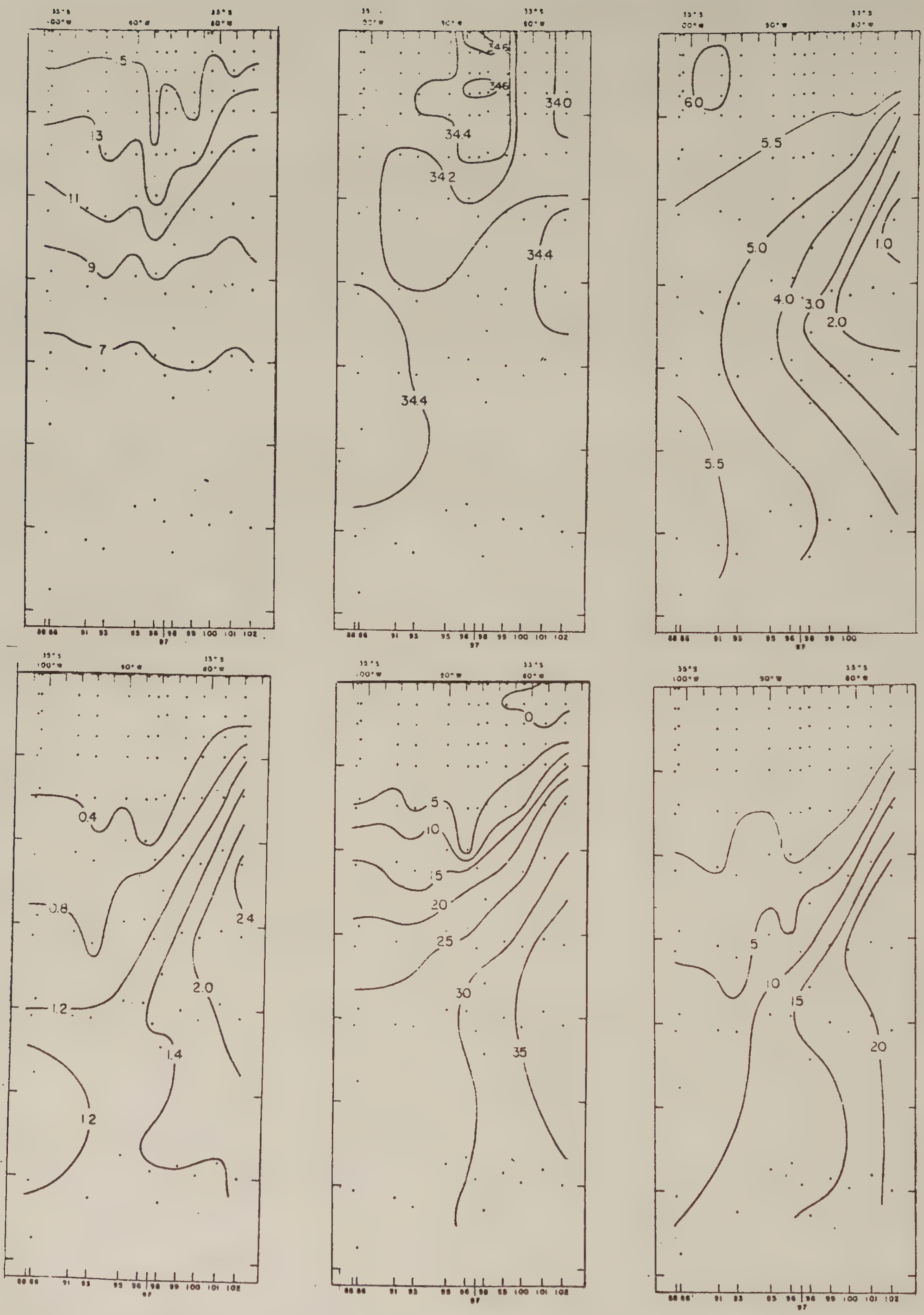


Fig. 10.- Secciones: a) temperatura, b) salinidad, c) oxígeno disuelto, d) fosfatos, e) nitratos y f) silicatos frente a Valparaíso, Chile, en noviembre de 1963 (de Forsbergh y Broenkow, 1965).

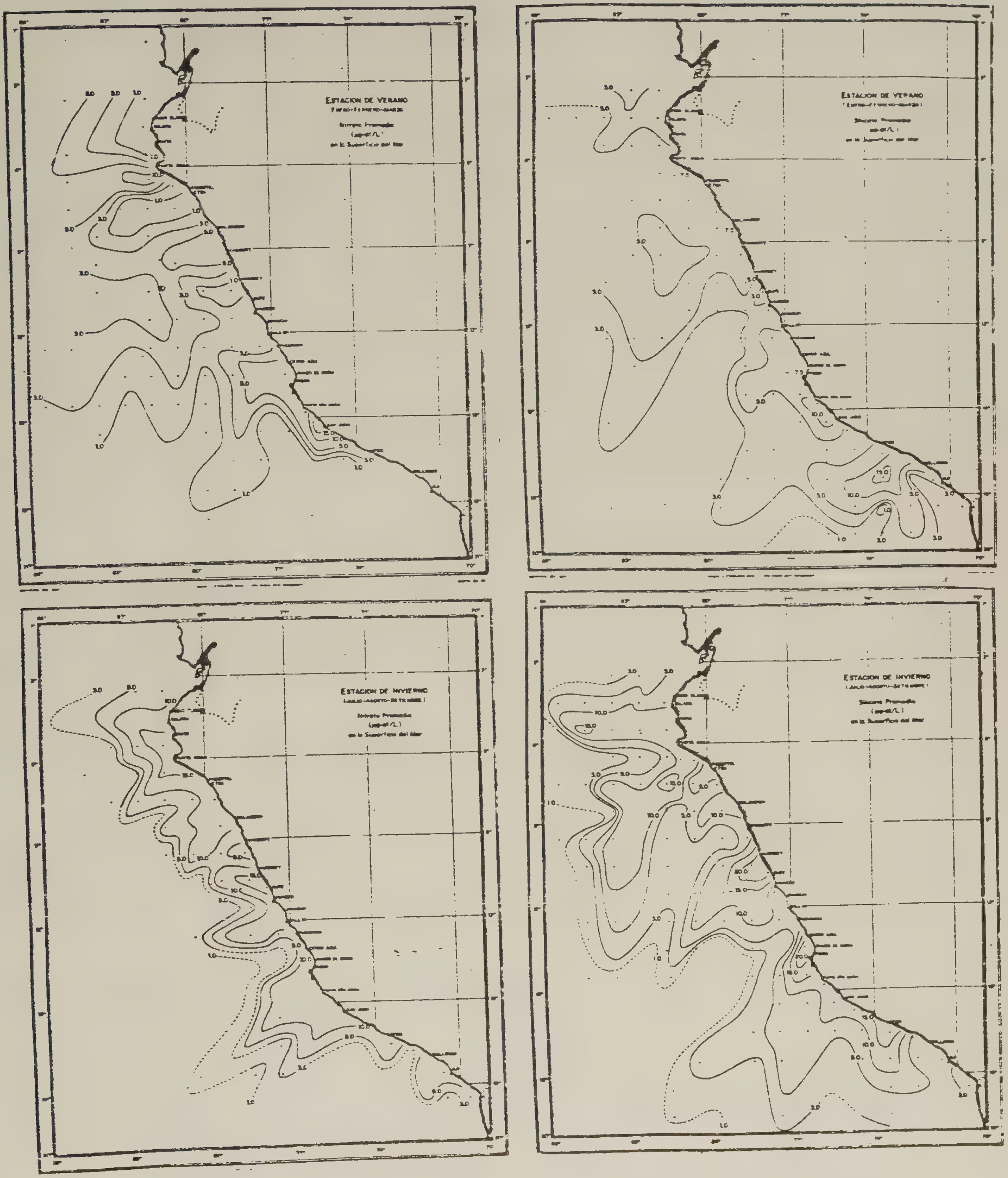

ESTACION DE VERANO
(Enero-Febrero-Marzo)
Nitrato Promedio
(ug-at/L)
en la Superficie del Mar
ESTACION DE VERANO
(Enero-Febrero-Marzo)
Silicato Promedio
(ug-at/L)
en la Superficie del Mar
ESTACION DE INVIERNO
(Julio-Agosto-Setiembre)
Nitrato Promedio
(ug-at/L)
en la Superficie del Mar
ESTACION DE INVIERNO
(Julio-Agosto-Setiembre)
Silicato Promedio
(ug-at/L)
en la Superficie del Mar

Fig. 11.- Nitratos y silicatos promedios a 0m en verano e invierno.

Frente a las costas del Perú (Guillén, 1976) la elevada concentración de nutrientes (Figs. 11 y 12) se debe en parte al afloramiento costero y en parte al transporte del agua de mezcla. En la superficie del mar se encontraron valores promedios de: 0.2 a 3.20 ug-at/L de fosfatos, 00 a 24.0 ug-at/L de silicatos y 0.5 a 21.0 ug-at/L de nitratos, hallándose los valores más altos cerca de la costa (>2.5 ug-at/L de fosfatos, >15.0 ug-at/L de silicatos y >15.0 ug-at/L de nitratos).

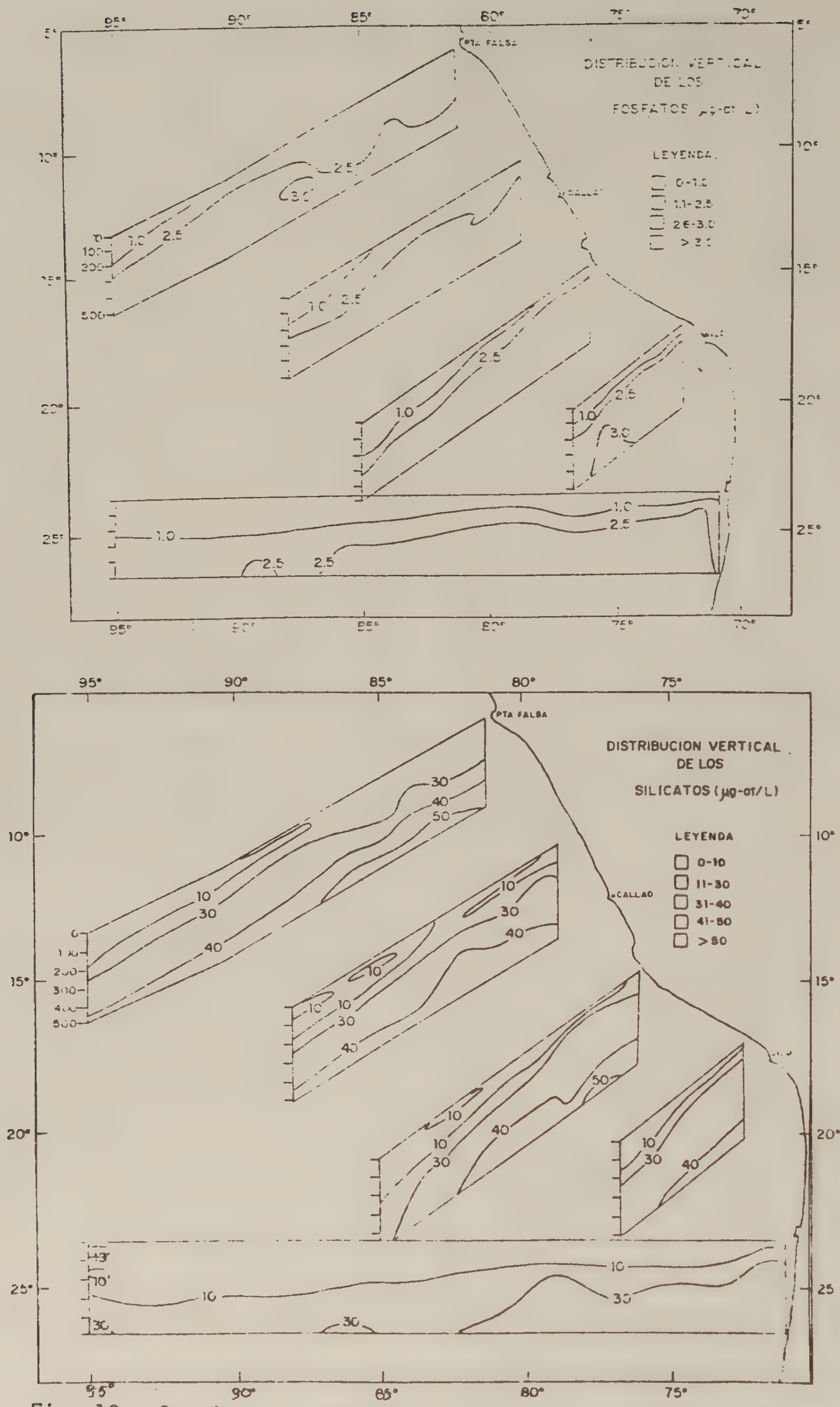

DISTRIBUCION VERTICAL
DE LOS
FOSFATOS (µg-at/L)
LEYENDA
0-1.0
1.1-2.5
2.6-3.0
> 3.0
PTA FALSA
CALLAO
1.0
2.5
3.0
DISTRIBUCION VERTICAL
DE LOS
SILICATOS (µg-at/L)
LEYENDA
☐ 0-10
☐ 11-30
☐ 31-40
☐ 41-50
☐ > 50
10
30
40
50
95°
90°
85°
80°
75°
70°
5°
10°
15°
20°
25°

Fig. 12.- Secciones de fosfatos y silicatos en octubre-noviembre de 1960.

Las menores concentraciones ($<$1.0 ug-at/L de fosfatos, $<$5.0 ug-at/L de silicatos y $<$5.0 ug-at/L de nitratos) se observaron en las Aguas Subtropicales Superficiales y Aguas Ecuatoriales Superficiales.

Frente al Panamá Bight no se dispone de mucha información sobre nutrientes, motivo por el cual sólo nos referimos a los resultados de los cruceros realizados durante la Operación ACENTO. En la superficie del mar la concentración de los nutrientes fueron muy bajas. Los fosfatos en la superficie del mar se encontraron con valores menores de 0.2 ug-at/L en la mayor parte del área durante todos los cruceros con un rango de 0.44 a 0.02 ug-at/L a excepción del ACENTO 4, donde se hallaron valores mayores de 0.02 ug-at/L, con una concentración máxima de 0.44 ug-at/L. Thomas (1966) señala que los nitratos son los más importantes de los micronutrientes en el Pacífico Oriental Tropical. Los nitratos en la superficie del mar se hallaron con concentraciones menores de 1.0 ug-at/L, con un rango de 0.0 a 3.2 ug-at/L. Los silicatos presentaron valores menores de 2 ug-at/L en la mayor parte del área. Parra (1977) y Forsbergh y Broenkow (1965) hallaron en la superficie del mar (Fig. 13) un rango de 0.2 a 4.5, 1.0 a 5.0 y 3.0 a 30.3 ug-at/L de fosfatos, nitratos y silicatos, respectivamente, para los meses de abril-mayo y septiembre-octubre de 1976. Forsbergh (1969) y Parra (1977) hacen un estudio más detallado para el área. Frente al Ecuador la información sobre nutrientes es limitada. En la superficie del mar las concentraciones de fosfatos son relativamente bajas y se presentan con valores de 0.05 a 1.55 ug-at/L al oeste de las Islas Galápagos, correspondiendo las mayores concentraciones al este de los 88°W. Los silicatos en la superficie del mar se hallaron con concentraciones de 0.10 a 20.0 ug-at/L.

FLUCTUACIONES DE LAS CONDICIONES OCEANOGRAFICAS

Condiciones Oceanográficas Durante Años Fríos

En los últimos 20 años, según la distribución de las anomalías térmicas se tiene los siguientes años fríos: 1964, 1967-68, 1970-71 y 1974-75, con anomalías negativas mayores de 2°C. Como ejemplo se ha seleccionado el año 1967, cuyas principales características son las siguientes.

La distribución de la temperatura y salinidad en la superficie del mar durante el verano e invierno son mostradas en las Figuras 3 y 4.

La Corriente Subsuperficial Ecuatorial (White, 1969) presenta dos ramales, uno al norte y otro al sur del Ecuador. Este último ingresa entre los 2° y 4°S y cerca de los 5°S el flujo dobla hacia el oeste hasta los 84°W donde se divide. Parte del flujo continúa hacia el oeste mientras que la mayor parte del flujo dobla hacia el sur, extendiéndose hasta cerca de los 10°S donde retorna a la costa. Allí el flujo dobla hacia el sur para formar la Corriente Subsuperficial Perú-Chile.

La Contracorriente Sur Ecuatorial (White, 1969) penetra a la región entre los 6° y 13° S, siendo su principal flujo entre los 6° y 8°S, asociado con una lengua de alto contenido de oxígeno mayor de 1.0 ml/L. Parte del flujo continúa hacia 84°W y cerca de los 5°S se junta con el flujo hacia el sur para formar la Corriente Subsuperficial Perú-Chile. Cochrane y Zuta (1969) mostraron un flujo hacia el este que tenía las mismas estructuras de masa de agua y dos cores de alta concentración de oxígeno cerca de 2°N y 2°S. Ambas ramas pasan en cada lado de las Islas Galápagos y se extienden hacia la costa de Sudamérica. Ellos sugirieron que la Contracorriente Sur Ecuatorial abastece de agua a la Corriente Subsuperficial Perú-Chile.

La distribución del oxígeno disuelto en la superficie de 180 cl/t (Fig. 14) está de acuerdo con la aceleración potencial a 160 cl/t, observándose el ramal sur de la Corriente Subsuperficial Ecuatorial. Wooster y Cromwell (1958) hallaron dos cores de alto contenido de oxígeno al este de las Islas Galápagos, una a 1°S y la otra a 2°N. Por otra parte, Bennett (1963) halló alto contenido de oxígeno en ambos lados de las Islas Galápagos y sólo al este de las islas a 84°W encontró un core de alto contenido de oxígeno sobre el Ecuador. Las dos lenguas de alto contenido de oxígeno observadas una a 79°W y otra a 87°W, está relacionada la primera con el flujo de la Corriente de Chile y la otra con el flujo hacia el oeste de la extensión de la Corriente de Chile.

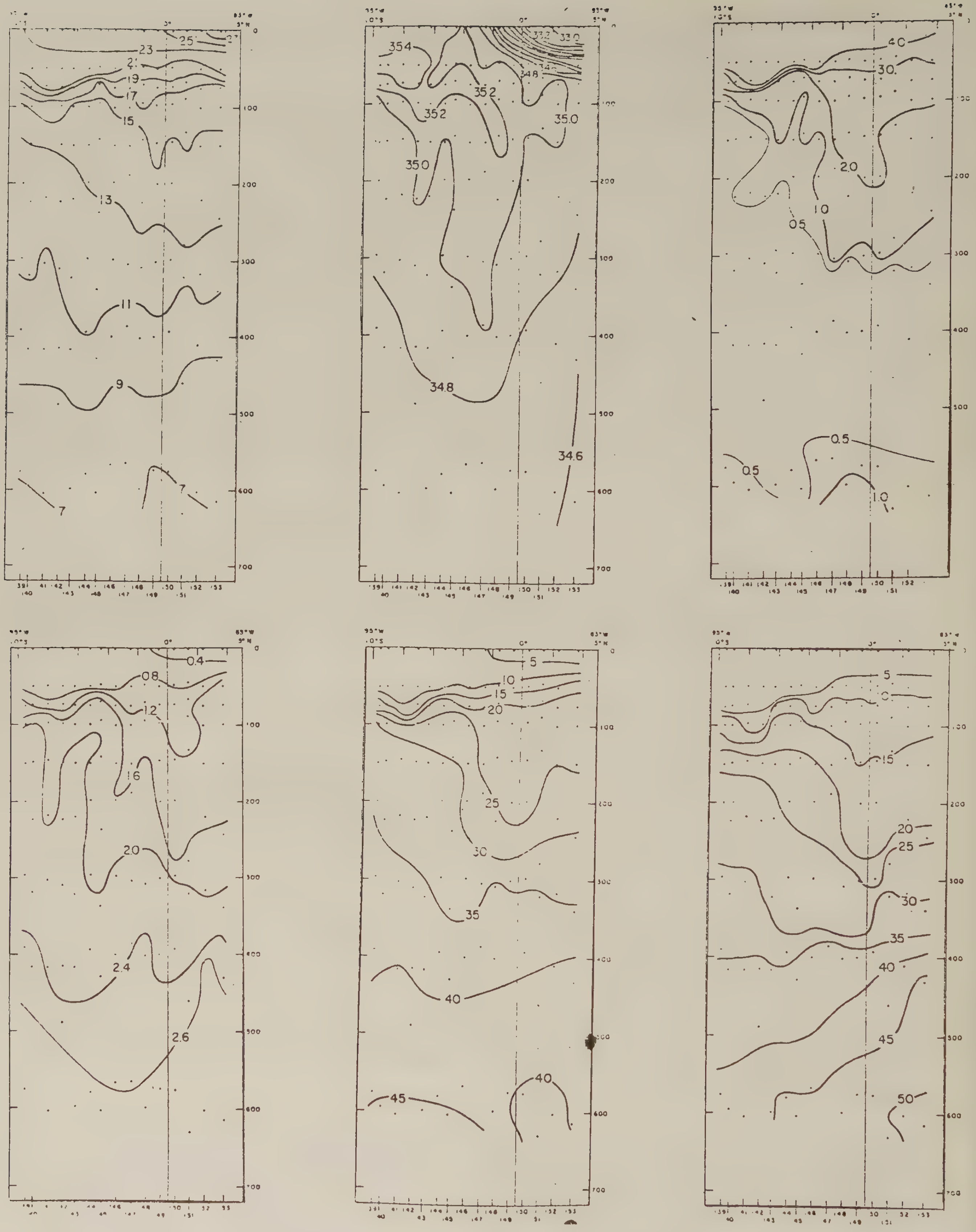


Fig. 13.- Secciones: a) temperatura, b) salinidad, c) oxígeno disuelto, d) fosfato, e) nitratos y f) silicatos frente a Colombia, Ecuador y Perú en diciembre de 1963 (de Forsbergh y Broenkow, 1965).

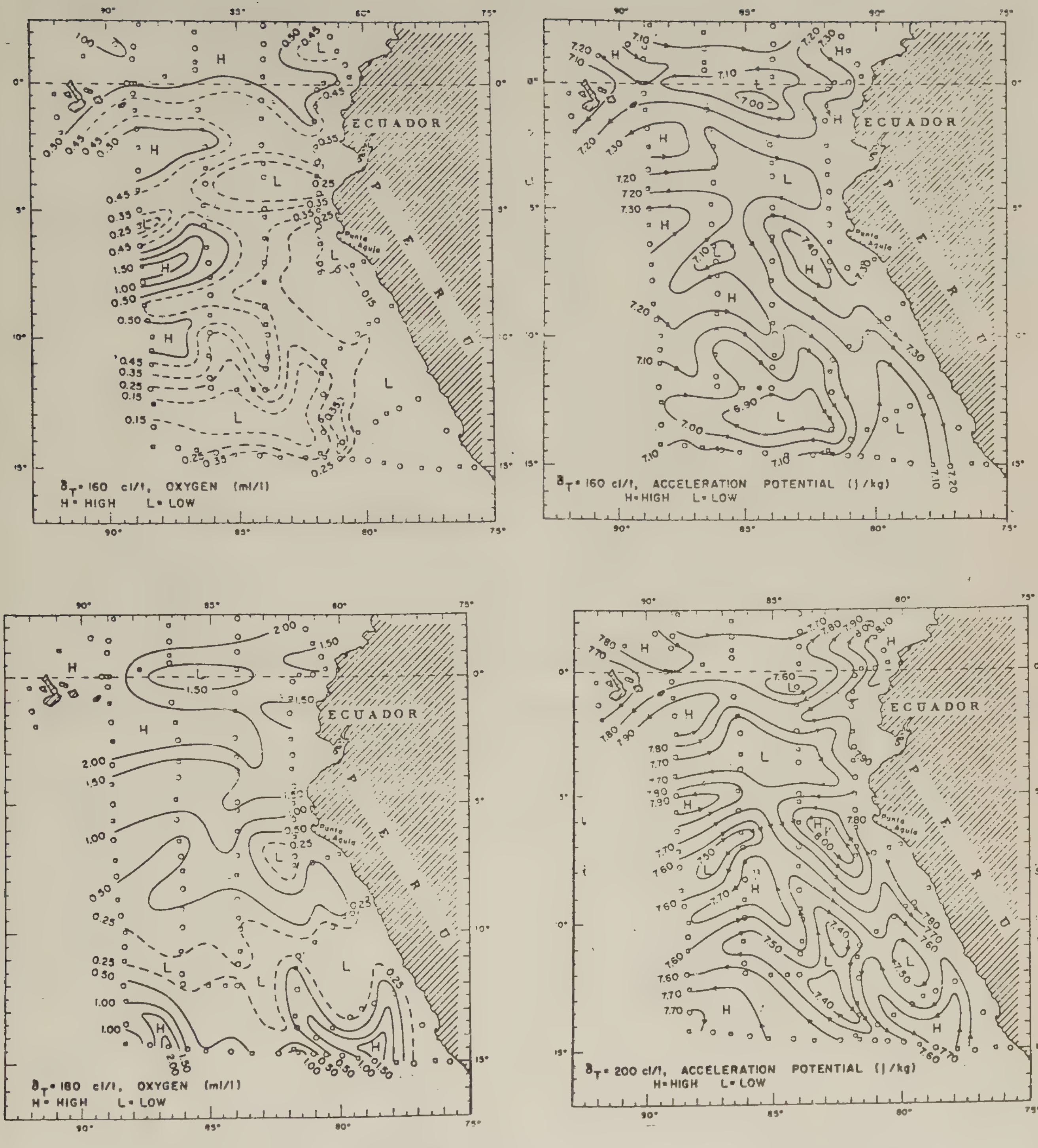

δ_T = 160 cl/t, OXYGEN (ml/l)
H = HIGH L = LOW
δ_T = 160 cl/t, ACCELERATION POTENTIAL (J/kg)
H = HIGH L = LOW
δ_T = 180 cl/t, OXYGEN (ml/l)
H = HIGH L = LOW
δ_T = 200 cl/t, ACCELERATION POTENTIAL (J/kg)
H = HIGH L = LOW
ECUADOR
PERU
Punta Aguja
90°
85°
80°
75°
0°
5°
10°
15°

Fig. 14.- Oxígeno disuelto a la superficie donde δ_T = 180 cl/t y aceleración potencial a la superficie donde δ_T = 200 cl/t en febrero-marzo de 1967 (de White, 1969).

La distribución de la acelaración potencial a 200 cl/t (Fig. 14) difiere un poco de la distribución a 160 cl/t (White, 1969) y muestra la rama sur de la Corriente Subsuperficial Ecuatorial, la que se extiende hacia la costa del Perú hasta cerca de 5ºS, donde la mayor parte del flujo fluye alrededor del meandro de Punta Aguja, mientras que el resto del flujo fluye fuera de la región a lo largo de 5ºS. Entre los 6º y 8ºS ingresa a la región la parte norte de la Contracorriente Surecuatorial.

Una gran parte de este flujo continúa hacia el este para juntarse al flujo hacia el sur del meandro de Punta Aguja. Dentro del meandro mismo se desarrolla un eddy anticiclónico, con un definido flujo hacia el norte. Entre los 10º y 11ºS ingresa a la región la parte sur de la Contracorriente Surecuatorial y se extiende al este hasta 84ºW.

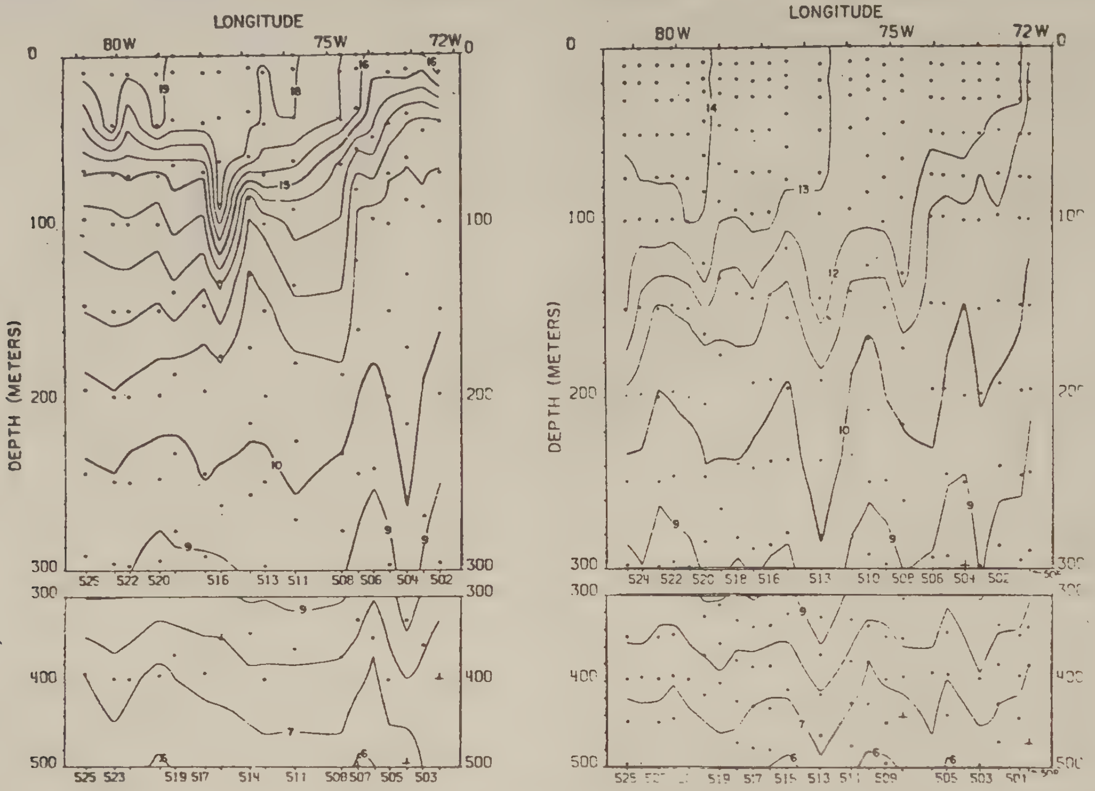


Fig. 15.- Secciones de temperatura frente a Valparaíso, Chile, en marzo y septiembre de 1967 (de Love, 1970-77).

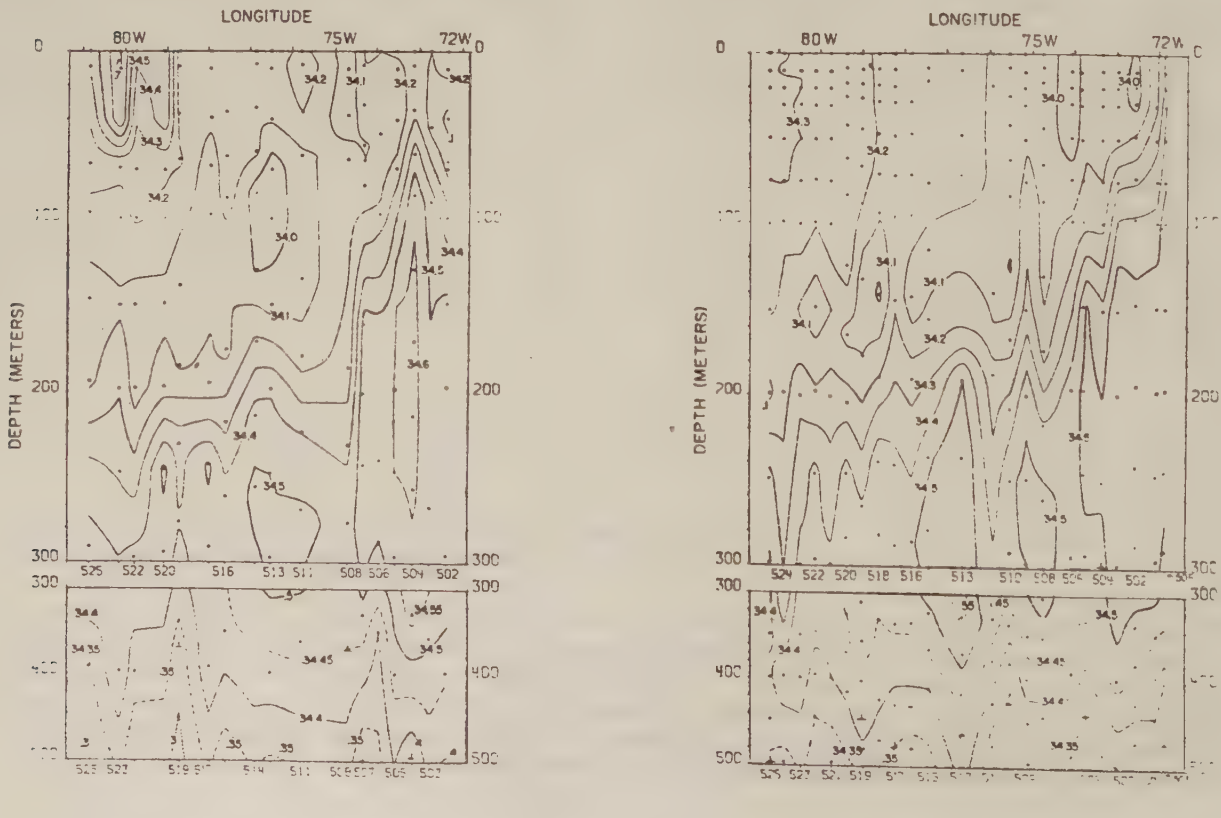


Fig. 16.- Secciones de salinidad frente a Valparaíso, Chile, en marzo y septiembre de 1967 (de Love, 1970-77).

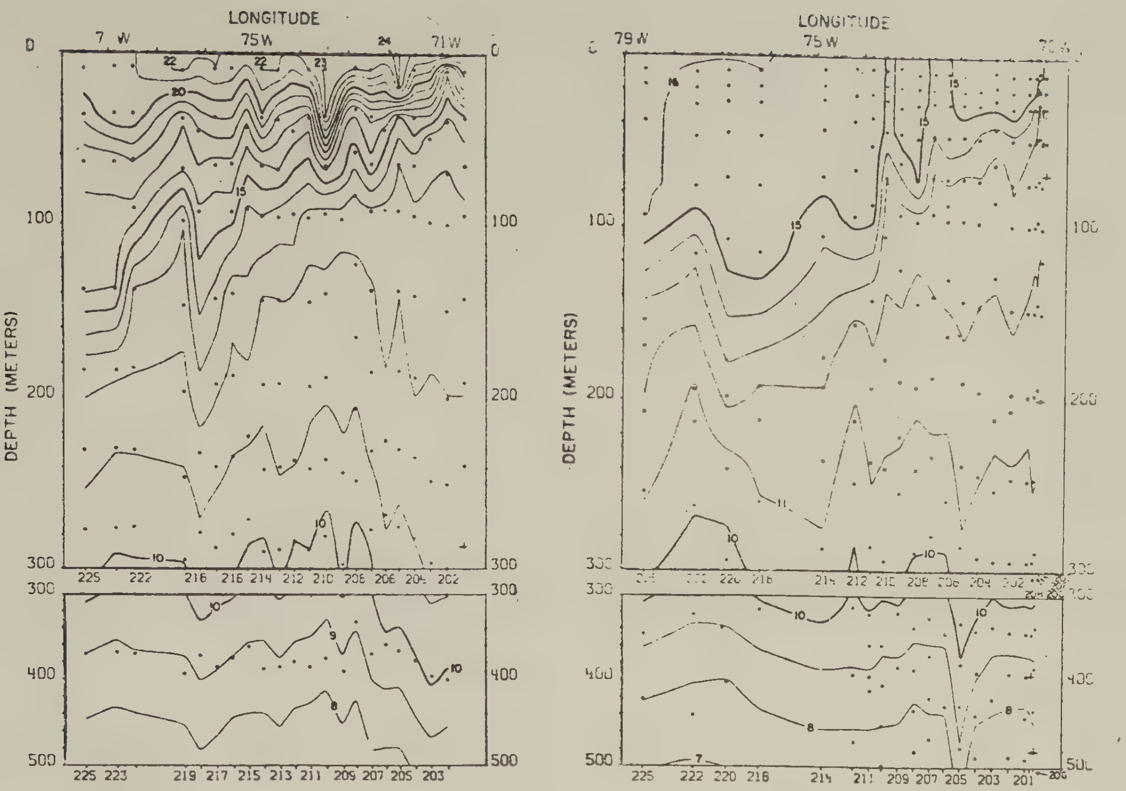


Fig. 17.- Secciones de temperatura frente a Iquique, Chile, en marzo y septiembre de 1967 (de Love, 1970-77).

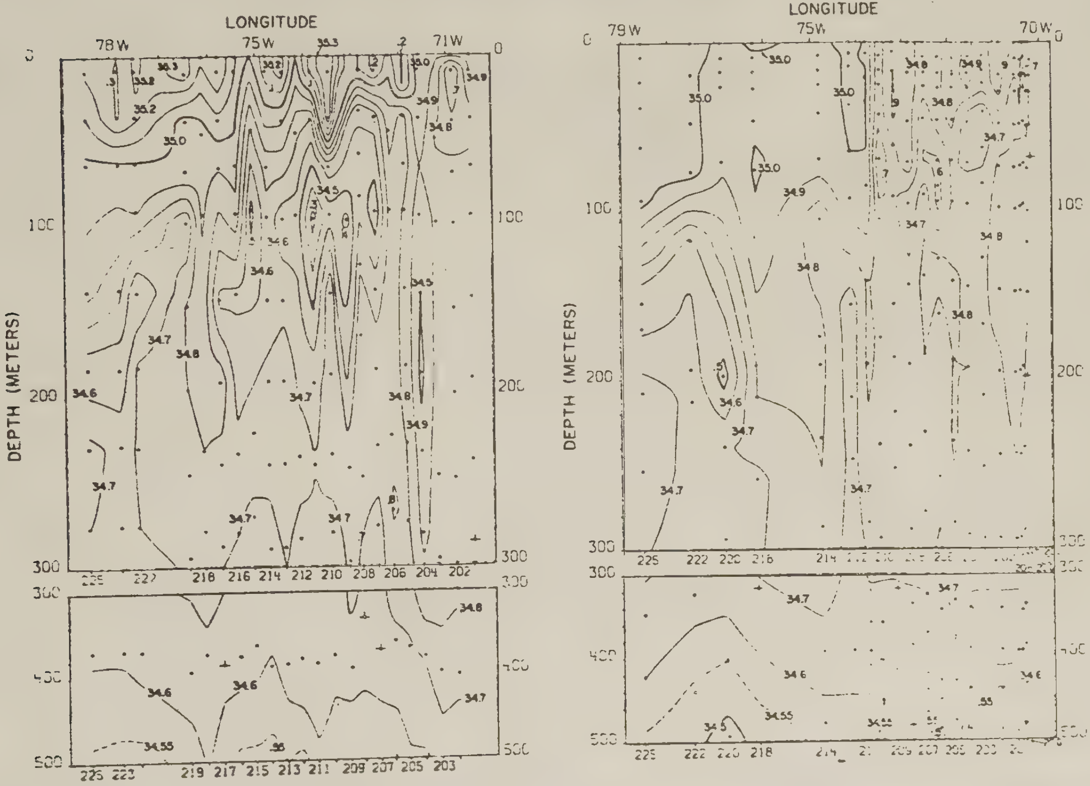


Fig. 18.- Secciones de salinidad frente a Iquique, Chile, en marzo y septiembre de 1967 (de Love, 1970-77).

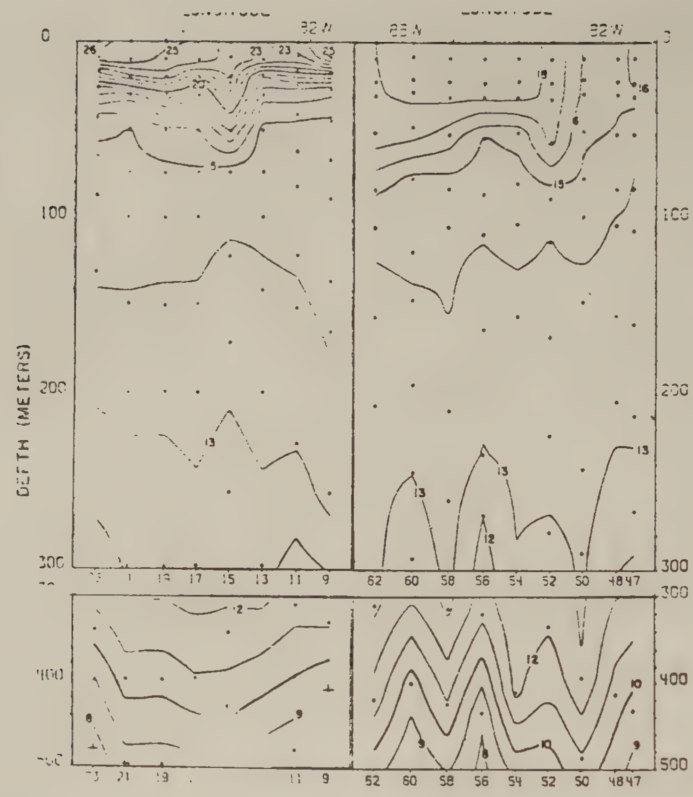


Fig. 19.- Secciones de temperatura frente a Cabo Blanco, Perú, en marzo y septiembre de 1967 (de Love, 1970-77).

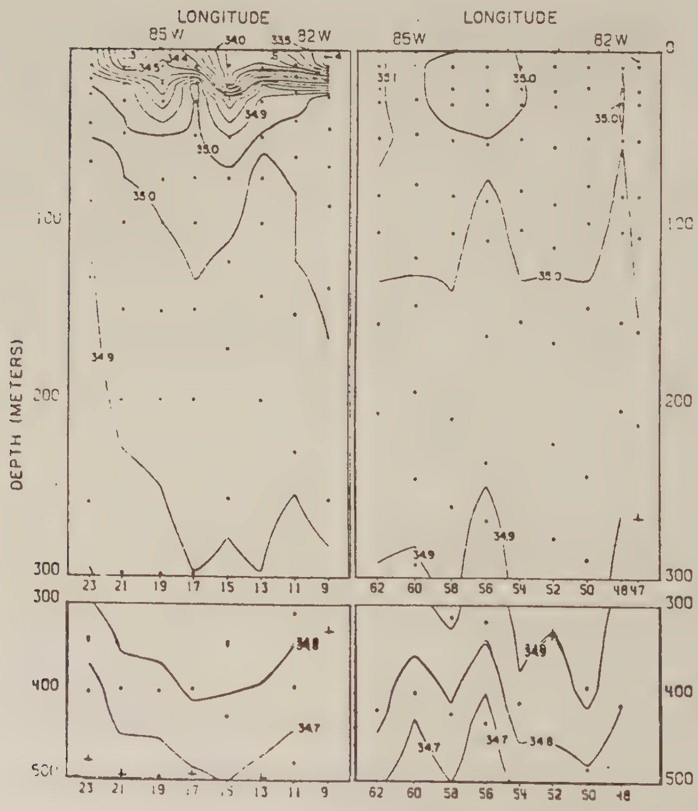


Fig. 20 .- Secciones de salinidad frente a Cabo Blanco, Perú, en marzo y septiembre de 1967 (de Love, 1970-77).

Para la distribución vertical de la salinidad y temperatura se han seleccionado las secciones frente a las latitudes 4°, 20° y 33°S (Figs. 15 a 20) en donde se destaca debajo de la capa superficial el flujo subsuperficial hacia el sur que tiene gran influencia en la circulación frente al Perú y Chile en la capa de 50 a 300 m de profundidad. La Corriente Subsuperficial Peruano-Chilena que se caracteriza por su salinidad relativamente alta, se hace más evidente al sur de los 15°S; así, frente a la latitud 20°S se presenta con salinidades mayores de 34.8 o/oo cerca de la costa y frente a la latitud 33°S con salinidades mayores de 34.5 o/oo en el verano (Fig. 16).

Otro flujo importante, principalmente frente a la costa de Chile, son las aguas subantárticas que son transportadas hacia el norte y que llegan en algunas oportunidades hasta los 12°S (Zuta y Guillén, 1970), con salinidades menores de 34.1 o/oo frente a la latitud 33°S y salinidades menores de 34.6 o/oo frente a la latitud 20°S, durante el verano.

Las variaciones del verano al invierno son mostradas en las figuras 15 a 20 en la que no sólo se observan cambios en la posición y características de las diferentes masas de aguas, sino también la intensidad de los procesos de afloramiento del que depende en gran parte el desarrollo de las pesquerías. Las aguas que afloran juegan un rol importante en la productividad de las aguas debido a que cada masa de agua tiene sus propias características físicas, químicas y biológicas (Calienes y Guillén, 1981); así por ejemplo, frente a la latitud 4°S en el invierno, las aguas que afloran corresponden a las aguas de la extensión de la Corriente de Cromwell, y las aguas que afloran frente a la latitud 20°S en el invierno, corresponden a las aguas subantárticas.

La rama sur de la Corriente Subsuperficial Ecuatorial (Figs. 21 a 23) es identificada no sólo por su termostato, sino también por su alto contenido de oxígeno y contenidos de nutrientes, los que presentan variaciones estacionales. La capa mínima de oxígeno disuelto de $<$0.25 también presenta variaciones no sólo en su extensión sino también en su espesor (Fig. 22). Los nutrientes también presentaron variaciones estacionales (Fig. 23), así los nitratros se hallaron entre 20 y 25 ug-at/L en el verano, aumentando de 25 a 30 ug-at/L en el invierno.

Condiciones Oceanográficas Durante Años Calientes

El Fenómeno El Niño aparece irregularmente frente a las costas de Sudamérica con grandes repercusiones en los niveles tróficos del ecosistema marino, afectando grandemente el rendimiento de las pesquerías. Los principales eventos ocurridos son: 1891, 1925-26, 1940-41, 1957-58, 1965, 1972-73, 1976 y 1982-83, los que tuvieron efectos limitativos en la producción biológica.

El Niño de 1965, se presentó frente a las costas del Perú (Guillén y Calienes, 1981) con mayor intensidad durante los meses de marzo y abril y fue causado por la invasión de Aguas Ecuatoriales Superficiales, caracterizada por temperaturas de 24°-27°C, salinidades de 33.0 a 34.8 o/oo, asociado con bajas concentraciones de nutrientes, de clorofila "a" (0.18-1.0 ug/l) y de productividad ($<$0.05 gC/m^2/día).

Durante El Niño de 1972, se observó dos desplazamientos de agua hacia el sur transportando aguas del Golfo de Panamá por el este de los 85°W, siendo el de febrero-marzo el más alejado de la costa, mientras que el de diciembre fue más costero (Zuta *et al.*, 1976).

Frente al Perú la primera fase tuvo lugar en febrero-marzo y fue caracterizado por la invasión de las aguas ecuatoriales hasta la latitud de 10°S, aproximadamente (Salinidad$<$34.5 o/oo) y bajas concentraciones de nutrientes (2.0-4.0 ug-at/L de silicatos, 0.50-0.75 ug-at/L de fosfatos y 0.75-1.00 ug-at/L de nitratos). Su contenido de clorofila "a" fue menor que la encontrada en El Niño de 1965. La producción total fue la tercera parte del promedio. La segunda fase apareció en diciembre en donde las aguas procedentes de la región ecuatorial se extendieron hasta los 10°S, aproximadamente, con temperaturas de 23-25°C y salinidad de 34.0 - 34.8 o/oo, asociado con bajas concentraciones de nutrientes y clorofila "a".

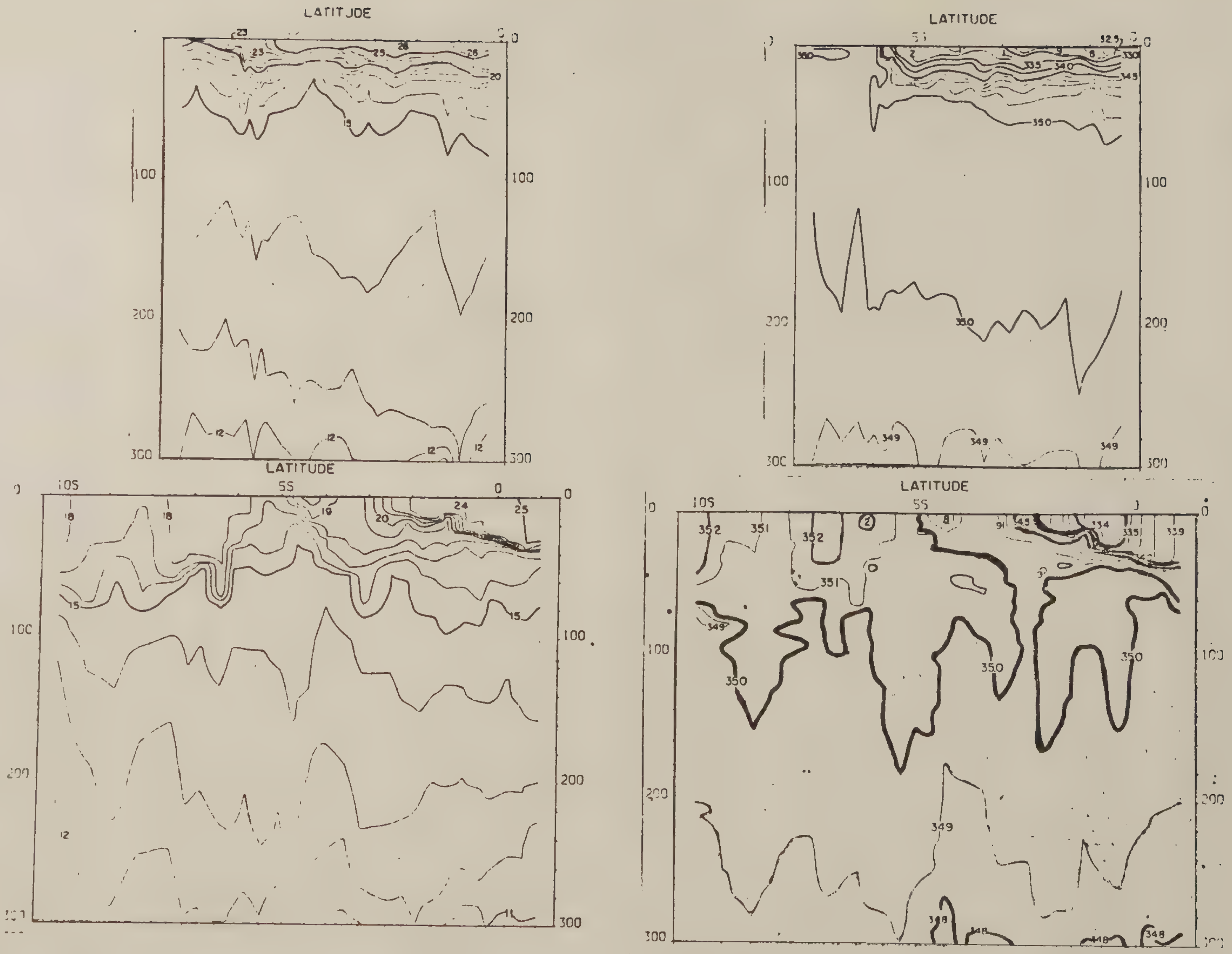


Fig. 21.- Secciones de temperatura a lo largo de 82ºW en febrero y agosto de 1967, 1970-77.

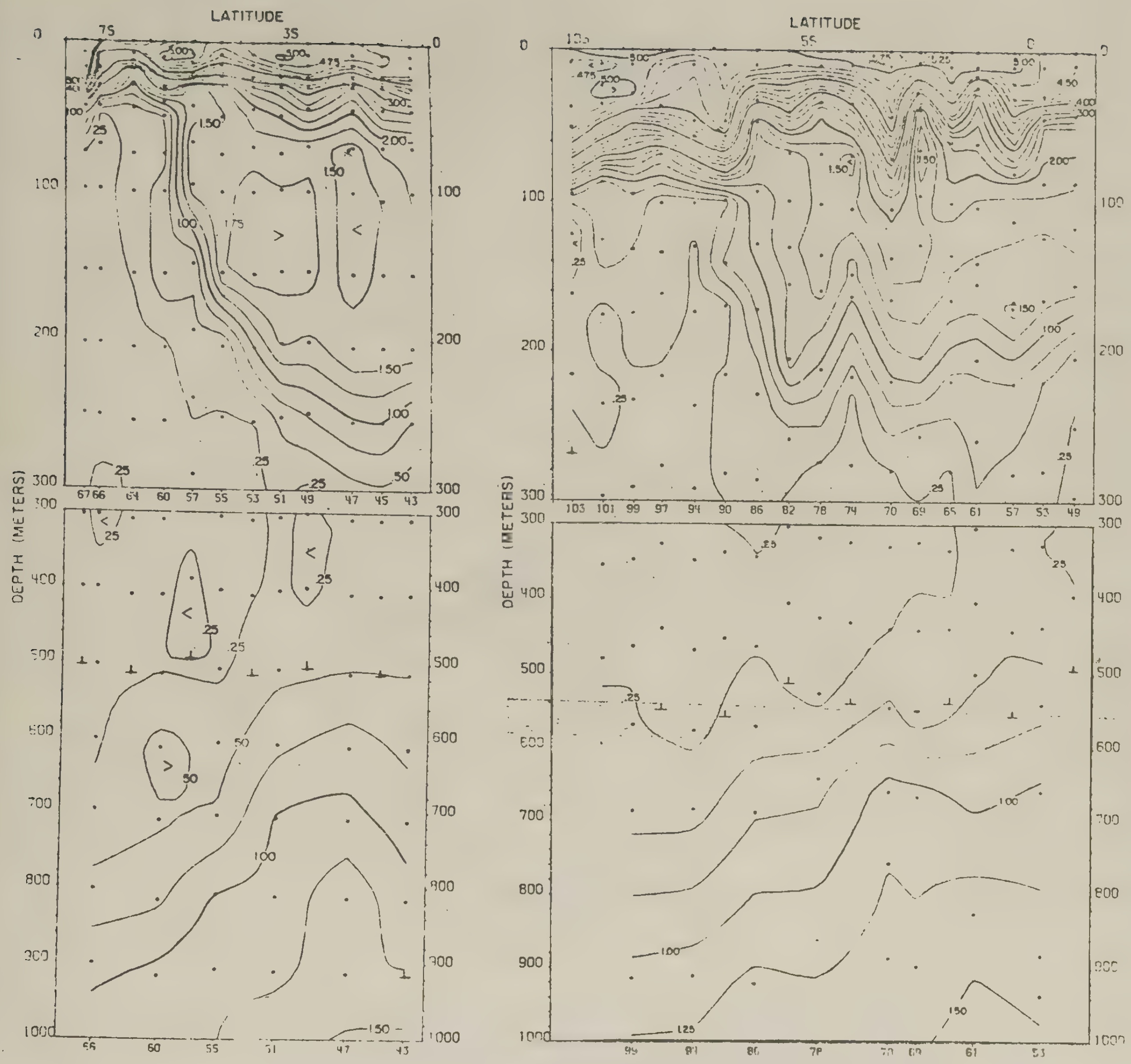


Fig. 22.- Secciones de oxígeno disuelto (ml/l) a lo largo de 82ºW en febrero y agosto de 1967 (de Love, 1970-77).

Frente a Chile, durante el verano, la temperatura superficial del mar se halló ligeramente sobre el promedio (Caviedes, 1981). Sin embargo, al sur de los 28ºS El Niño no tuvo influencia (Alarcón, 1975).

El invierno de 1972 se caracterizó por el predominio de las Aguas Subtropicales Superficiales (salinidad >35.1 o/oo) frente a la costa peruana al sur de los 5ºS y al oeste de los 83ºW frente al Ecuador. Las Aguas Tropicales Superficiales avanzaron en dos frentes, uno costero que se extendió hasta los 4ºS y otro lejos de la costa frente a Esmeralda que se extendió en dirección SW hasta los 2ºS.

Frente a Chile, las aguas se hallaron más calientes que lo normal, siendo más marcado en casi toda el área costera en donde predominaron las Aguas Subtropicales Superficiales con salinidades mayores de 35.0 o/oo, cuyas salinidades son más altas que las encontradas en 1967 (Robles *et al.*, 1976; y Sievers y Silva, 1976).

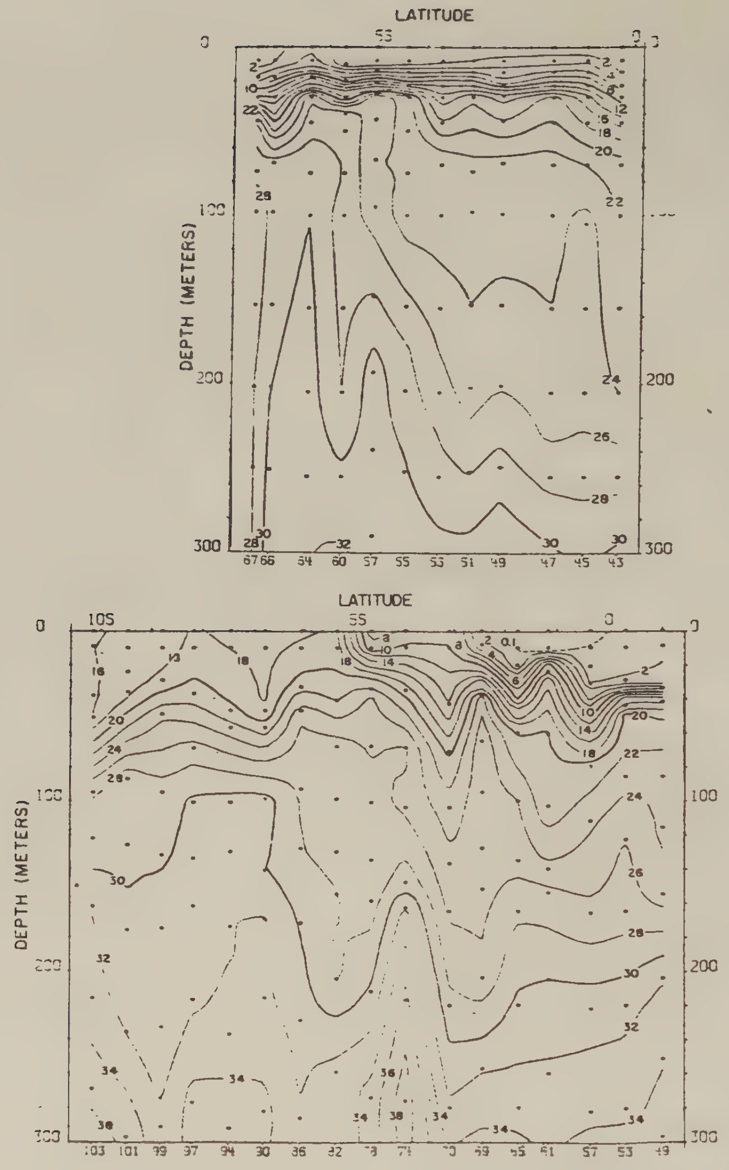


Fig. 23.- Secciones de nitratos (ug-at/l) a lo largo de 82°W en febrero y agosto de 1967 (de Love, 1970-77).

El Niño de 1976 frente a las costas de Perú, en enero y febrero se observó un calentamiento de la temperatura superficial del mar al norte de los 15°S, debido a la presencia de las Aguas Ecuatoriales Superficiales (salinidad< 34.8 o/oo) que se extendió hasta los 9°S. Sin embargo, el máximo calentamiento fue hallado en junio-agosto, asociado con Aguas Subtropicales Superficiales caracterizadas por su baja concentración en nutrientes y productividad. La distribución de la clorofila "a" fue muy diferente al promedio especialmente en julio con valores 1.0 ug/L en casi toda la costa.

El Niño de 1982 frente al Perú (Zuta y Guillén, 1983), en el mes de septiembre se observó un calentamiento a lo largo de la costa con anomalías mayores de 2°C que el promedio, originado por la aproximación a la costa de las Aguas Subtropicales Superficiales, caracterizadas por su baja concentración en nutrientes y productividad, cuyo calentamiento continuó los próximos meses. En enero de 1983 (Fig. 24) se observó la presencia de aguas de la región ecuatorial (salinidad<34.8 o/oo) con temperaturas de 26°-29°C, que se extendieron hasta la latitud de 14°S aproximadamente, asociado con bajísimas concentraciones de nutrientes, (<6.0 ug-at/L de silicatos,<0.4 ug-at/L de nitratos, y<0.2 ug-at/L de fosfatos). Las concentraciones de los fosfatos y nitratos fueron inferiores a los encontradas en El Niño de 1972.

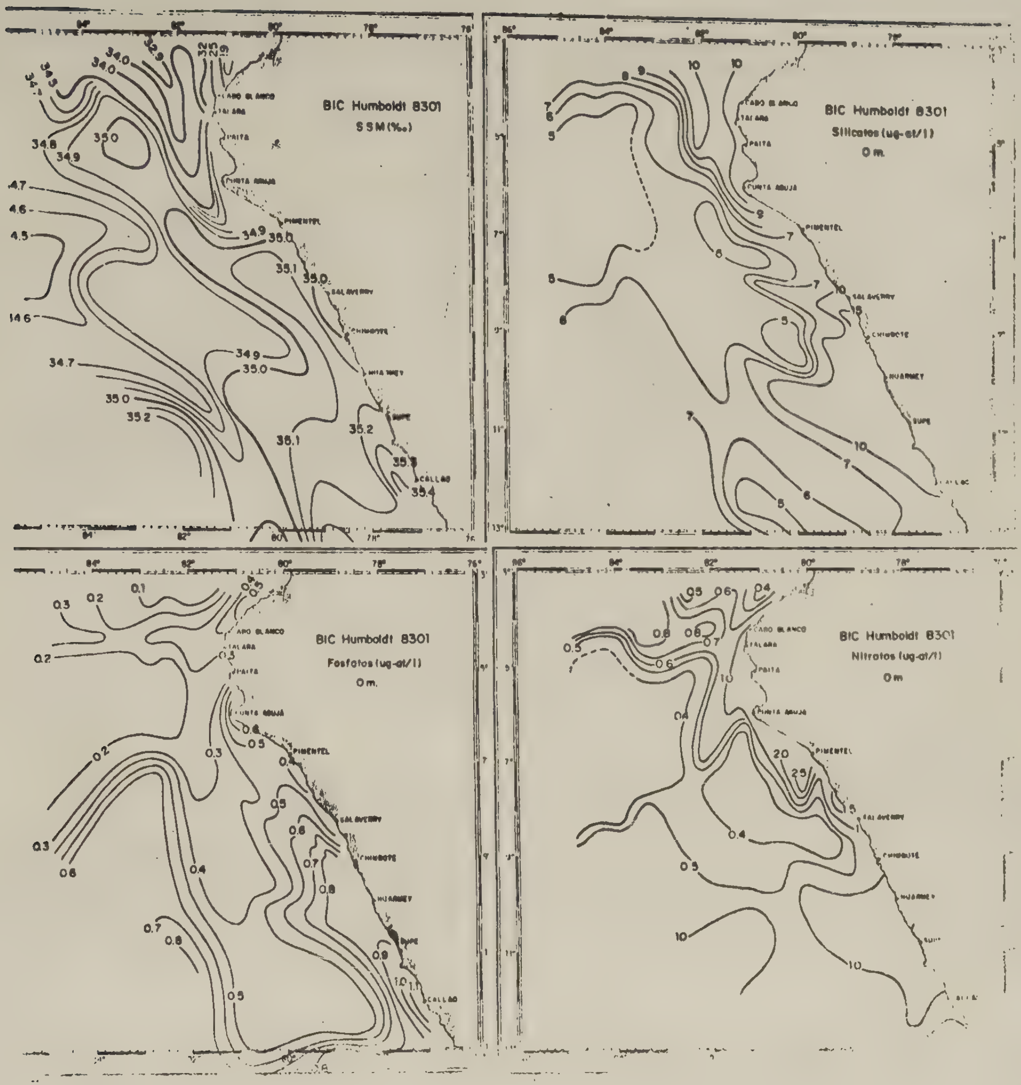

BIC Humboldt 8301
SSM (‰)
BIC Humboldt 8301
Silicatos (ug-at/l)
0 m
BIC Humboldt 8301
Fosfatos (ug-at/l)
0 m.
BIC Humboldt 8301
Nitratos (ug-at/l)
0 m
Cabo Blanco
Talara
Paita
Punta Aguja
Pimentel
Salaverry
Chimbote
Huarmey
Supe
Callao

Fig. 24.- Salinidad, fosfatos, silicatos y nitratos a Om en enero-febrero de 1982 (de Zuta y Guillén, 1983).

En 1975, en febrero-marzo (Wyrtki, 1976) hubo una transgresión de aguas (Fig. 25) de la región ecuatorial hacia el sureste, sin llegar a la costa peruana con características de un Niño, y luego se replegó en los meses de abril-mayo y fue considerado como un aborto de El Niño. Las Aguas Ecuatoriales Superficiales se hallaron con temperaturas mayores de 27ºC y salinidades menores de 34.5 o/oo, asociado con bajas concentraciones de nutrientes y producción primaria, inferiores al promedio. A pesar de su corta duración tuvo efectos en la productividad del área costera peruana y presentó cambios bien marcados no sólo en las propiedades físicas, sino también químicas y biológicas. Durante el otoño de 1975 frente a Chile, los afloramientos no estuvieron bien desarrollados (Basten, 1978) a pesar de que las temperaturas cerca de la costa fueron inferiores al promedio.

Durante el Fenómeno El Niño el afloramiento costero continúa, pero las aguas subsuperficiales que afloran son calientes y pobres en nutrientes, dando como resultado un decrecimiento de la cantidad de fitoplancton y un efecto adverso en el zooplancton, peces, etc. Comparando las áreas de afloramiento del Noroeste de Africa, Oregon y Perú, se tiene que de las 3 regiones solamente en el Perú ocurre El Niño, a pesar que los vientos costeros no disminuyen (Wyrtki, 1975) y los procesos del afloramiento costero continúan.

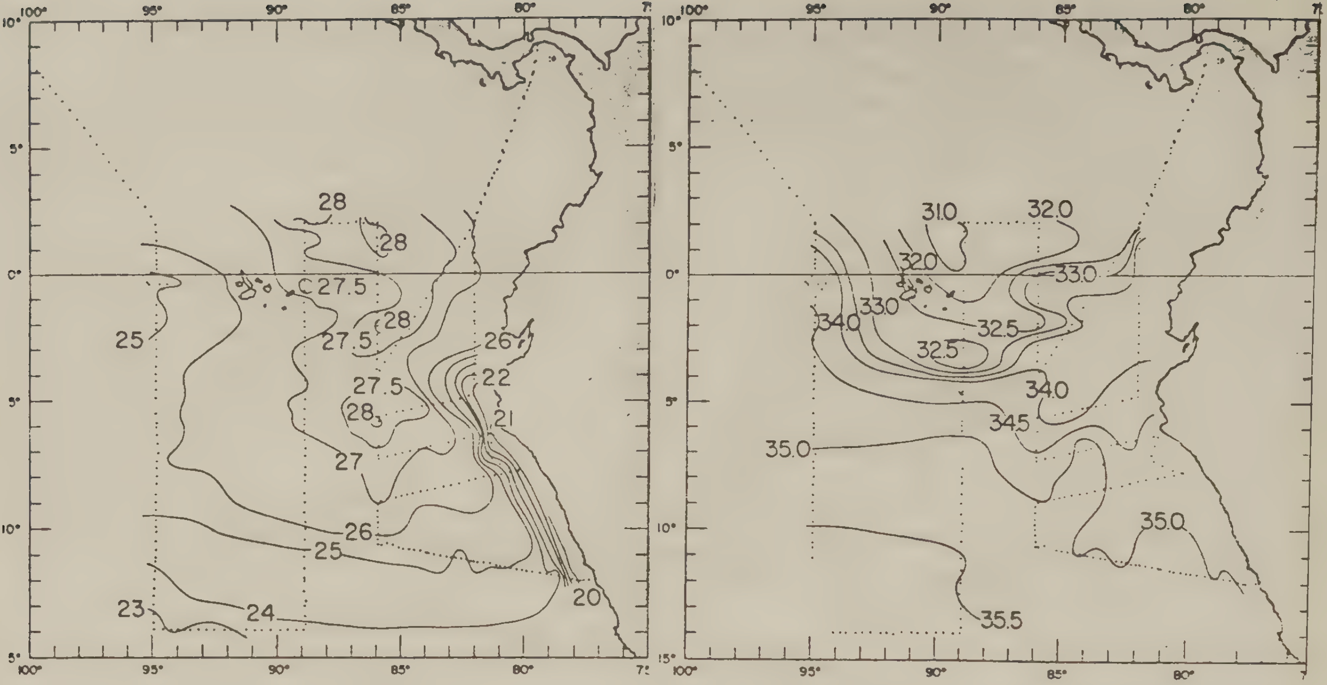


Fig. 25.- Temperatura y salinidad a 0m en febrero-marzo y abril-mayo de 1975 (de Pattert et al., 1978).

Variaciones Estacionales de las Condiciones Oceanográficas

Las variaciones estacionales tienen gran efecto en los diferentes niveles tróficos del ecosistema marino; y para mostrar estos cambios se han seleccionado secciones frente a Buenaventura, Galera, Islas Galápagos, Cabo Blanco y Arica, para el período 1964-1966 (Stevenson et al., 1970) en el que el año 1964 representa un año muy frío y el de 1965 un año de El Niño.

En la sección frente a Buenaventura, una de las características del Panamá Bight (parte del Pacífico Oriental Tropical comprendida por el meridiano 81ºW en el costado occidental, la entrada del Golfo de Panamá en el norte(71-72ºN) y el costado sur a lo largo de 1ºN) es la existencia de un domo termal que se puede observar por la curva ascendente de las isotermas que a veces llegan a la superficie. Dicho domo no señala necesariamente la presencia de afloramiento, ya que frecuentemente se encuentra debajo de la superficie.

La distribución estacional de la temperatura y salinidad superficial (Stevenson et al., 1970) sugiere que el domo se halla presente en la primavera del norte (febrero-marzo) y se encuentra centralizado cerca de los 5ºN.

Las secciones verticales de temperatura (Fig. 26) muestran la evidencia del domo. Las figuras 26 y 27 muestran las variaciones trimestrales en la distribución de temperatura, salinidad y concentración de oxígeno disuelto.

En las secciones frente a Galera e Islas Galápagos, entre las aguas tropicales de alta temperatura y baja salinidad del Bight y el agua fría y salina de la Corriente del Perú, se halla el límite frontal. El frente ecuatorial se extiende en dirección noroeste desde la frontera Ecuador-Perú hasta pasar al noreste de las Islas Galápagos, el cual es más intenso cerca a la costa, debilitándose gradualmente hacia el oeste. La distribución de la temperatura y salinidad en el frente ecuatorial varía estacionalmente y de un año a otro. Una característica del área es la presencia de una célula (Stevenson et al ., 1970) entre la costa y las Islas Galápagos cuyo tamaño y ocurrencia varía estacionalmente. El frente ecuatorial de enero a marzo es más meridional y débil, y la célula no está presente. En abril-junio cuando la velocidad de la Corriente del Perú aumenta puede formarse la célula. Las figuras 27 a 30 presentan las variaciones estacionales de la temperatura, salinidad y oxígeno disuelto. La variación de la Corriente Subsuperficial Ecuatorial, caracterizada por su termostato y relativamente alto contenido de oxígeno

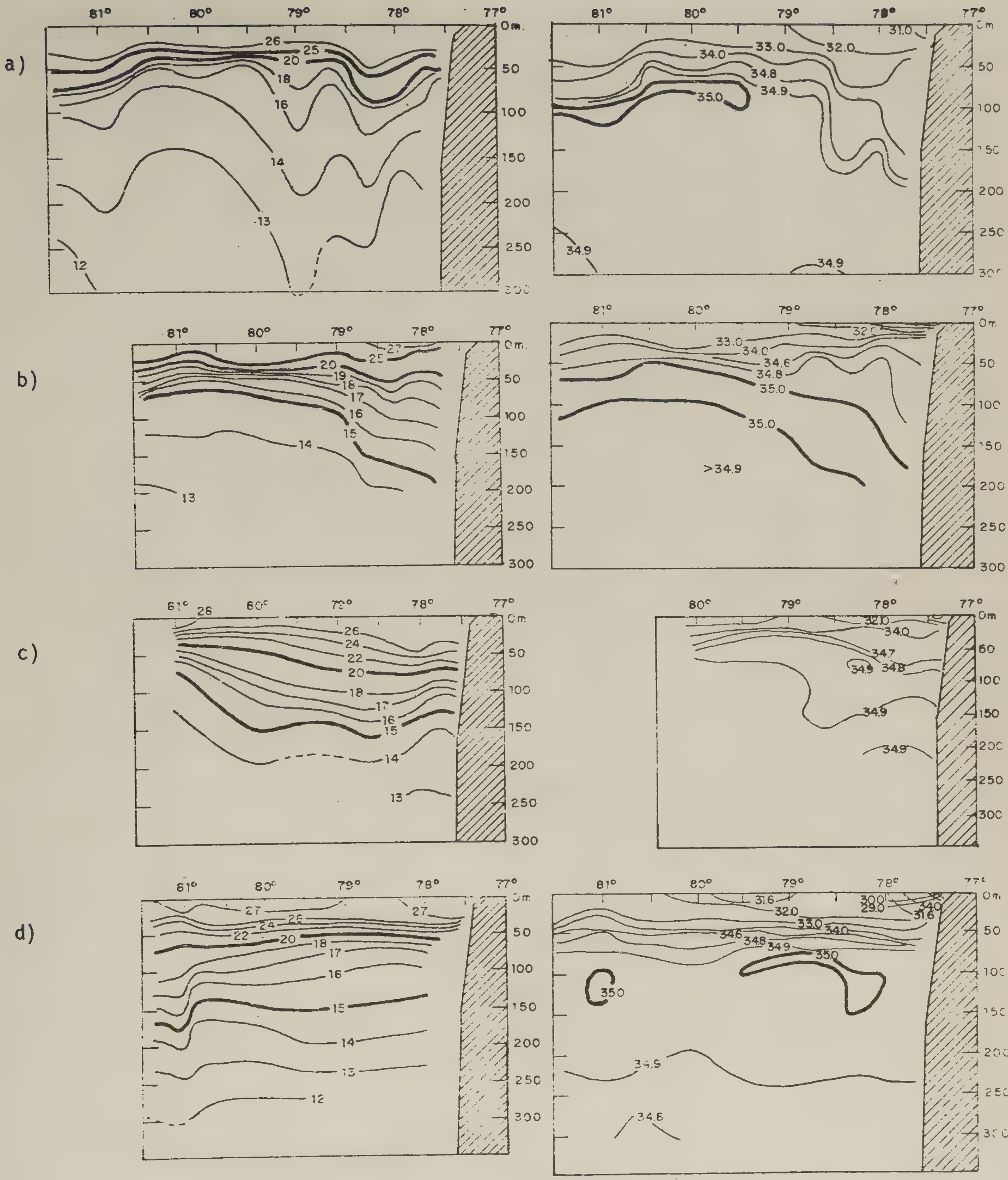


Fig. 26.- Secciones de temperatura y salinidad frente a Buenaventura: a) Cr. 64-4, b) Cr. 65-1, c) Cr. 65-2 y d) Cr. 65-3 (de Stevenson et al., 1970).

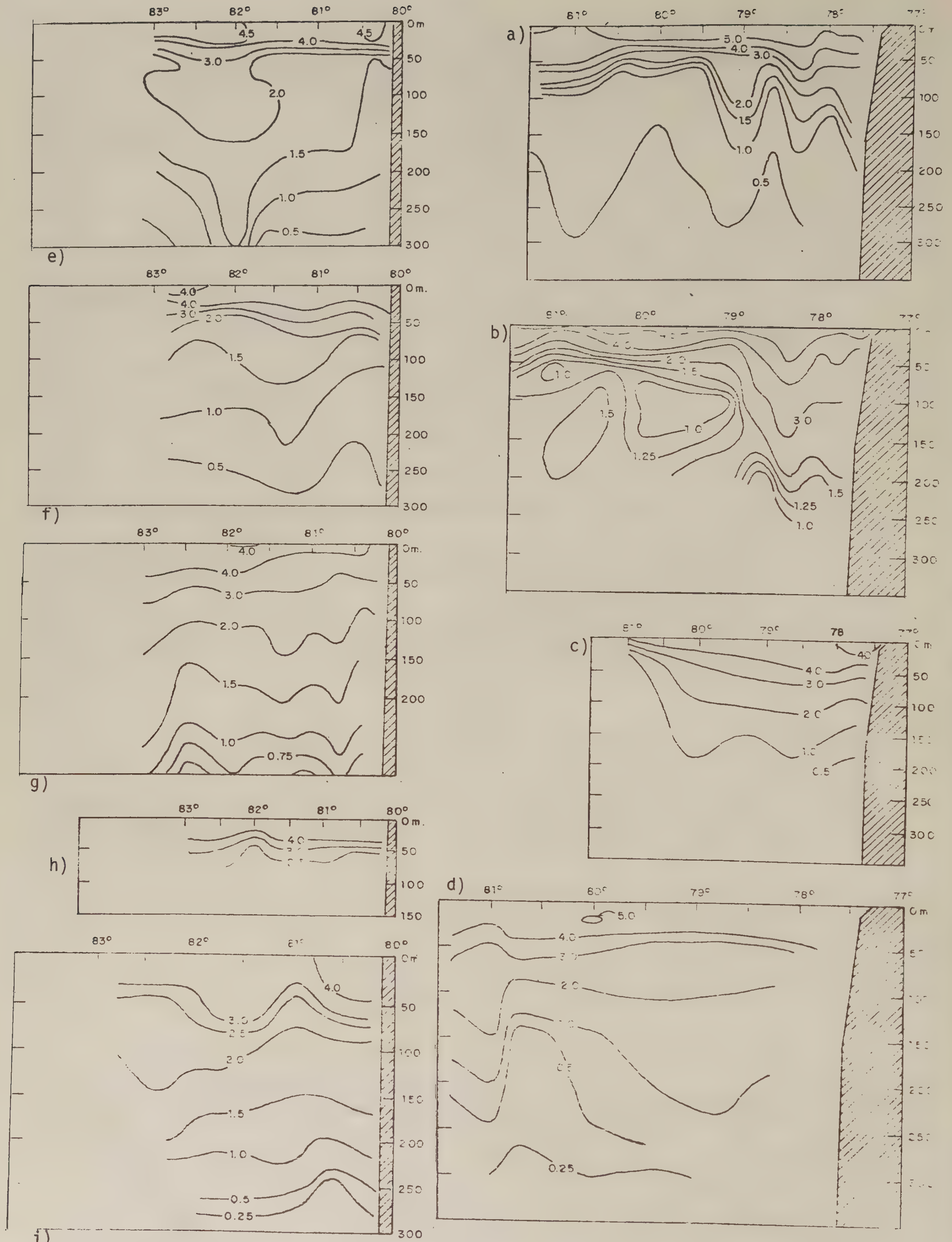


Fig. 27.- Secciones de oxígeno disuelto frente a Buenaventura y Galera: a) Cr. 64-4, b) Cr. 65-1, c) Cr. 65-2, d) Cr. 65-3, e) Cr. 64-3, f) Cr. 64-4, g) Cr. 65-1, h) Cr. 65-2, i) Cr. 65-3, (de Stevenson et al., 1970).

disuelto, es observada durante El Niño de 1965 en el que se presentó en el verano e intensificó a principios del otoño. Stevenson y Taft (1971) muestran que las aguas de la Corriente Subsuperficial Ecuatorial ingresa cerca del Ecuador hacia el este con velocidades de hasta 37 cm/seg y luego dobla hacia sureste cerca de los 83ºW y es hallado a 110 km de la costa del Ecuador y norte del Perú, caracterizada por su salinidad máxima de 35.13 - 36.17 o/oo y temperatura de 17.2ºC.

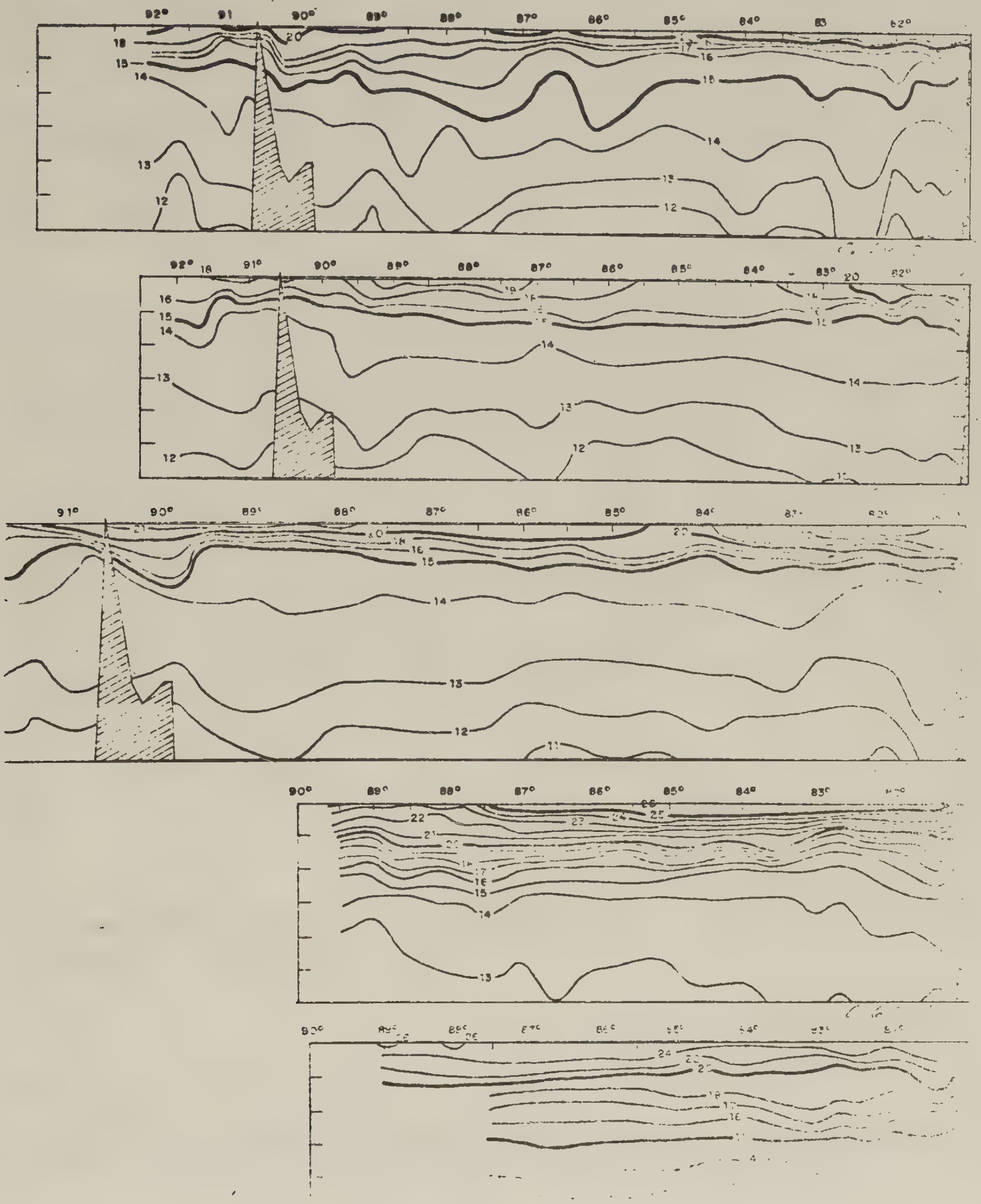


Fig. 28.- Secciones de temperatura frente a Galápagos: a) Cr. 64-2, b) Cr. 64-3, c) Cr. 64-4, d) Cr. 65-1 y e) Cr. 65-2 (de Stevenson et al., 1970).

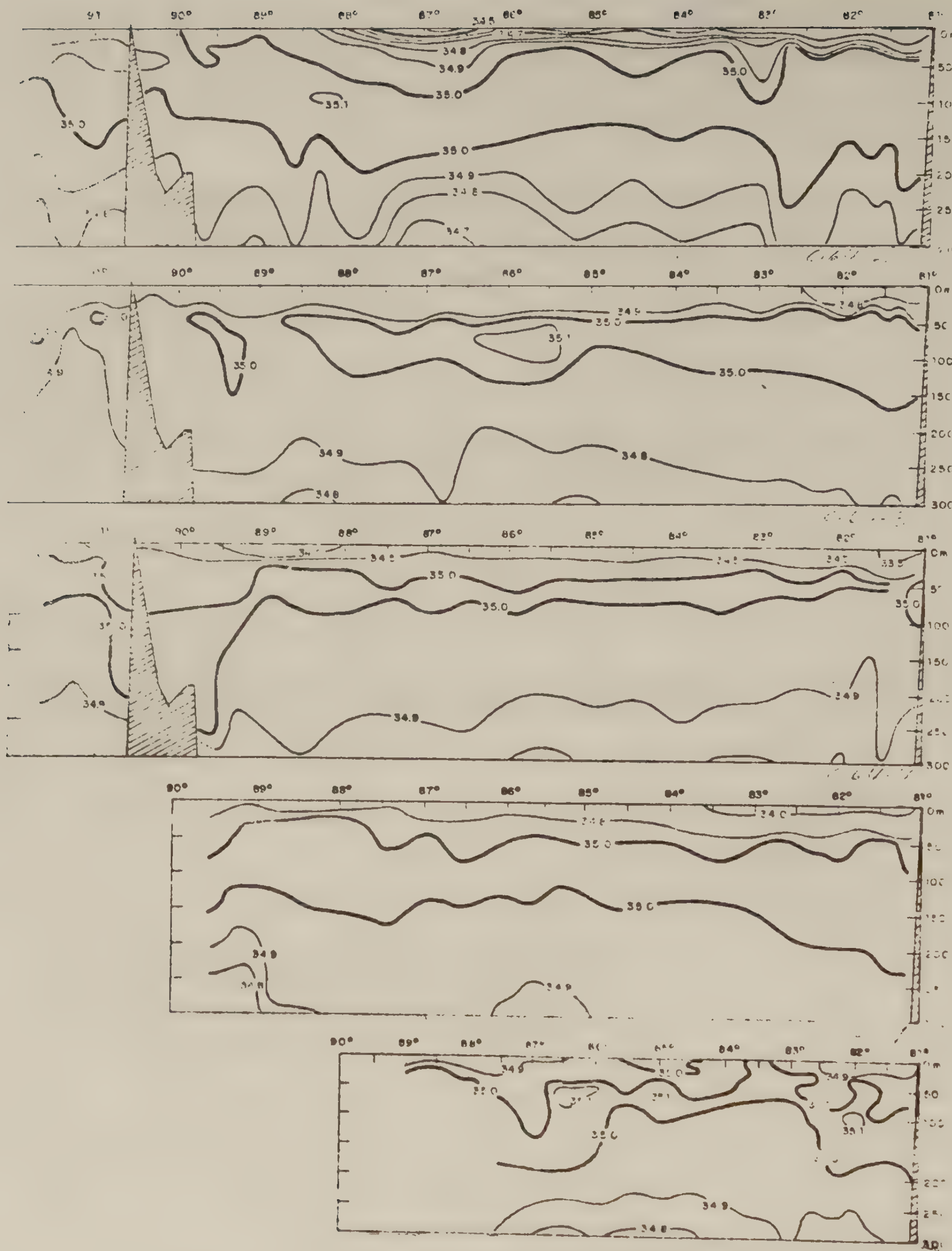


Fig. 29.- Secciones de salinidad frente a Galápagos: a) Cr. 64-2, b) Cr. 64-3, c) Cr. 64-4, d) Cr. 65-1 y e) Cr. 65-2 (de Stevenson et al., 1970).

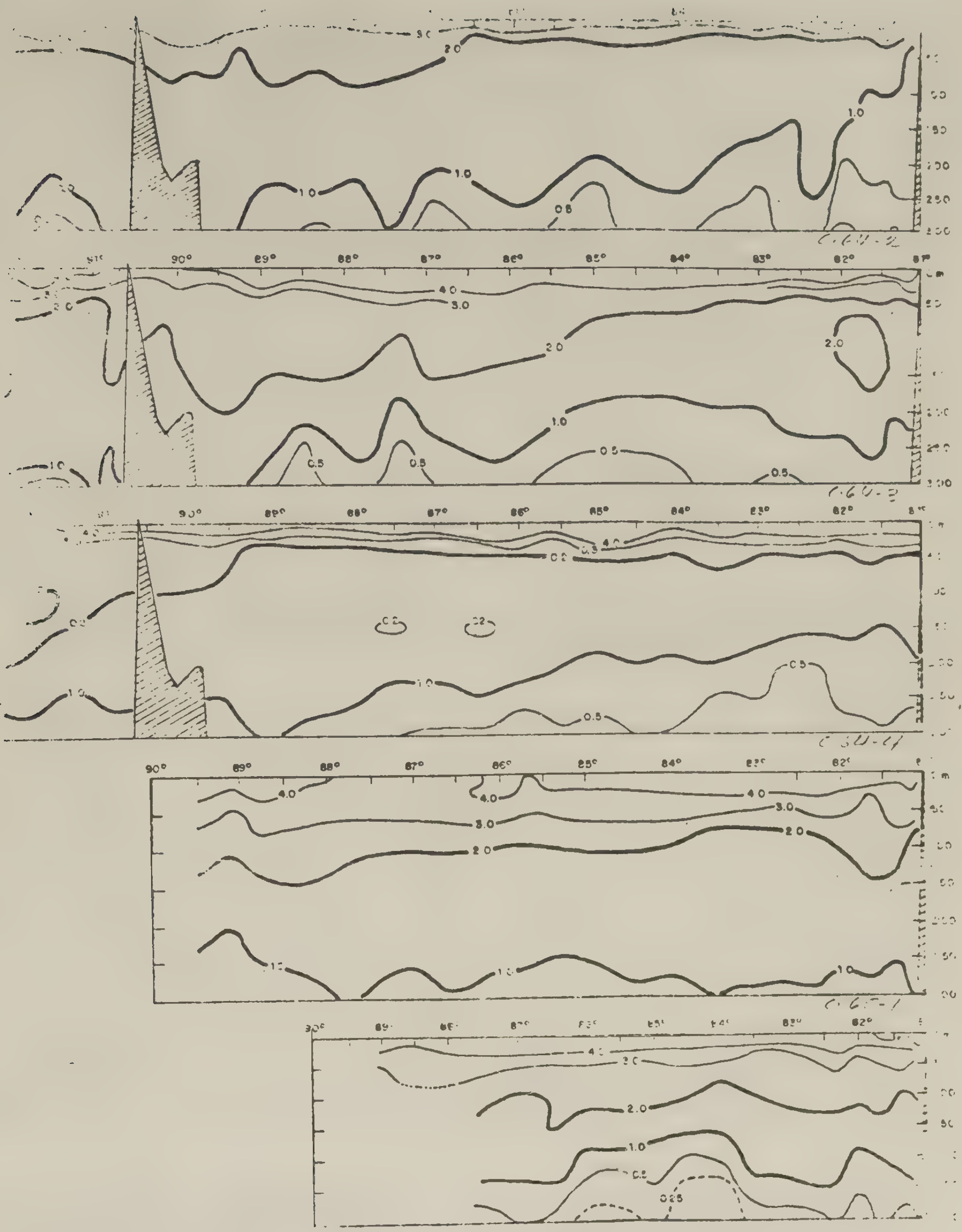


Fig. 30.- Secciones de oxígeno disuelto frente a Galápagos: a) Cr. 64-2, b) Cr. 64-3, c) Cr. 64-4, d) Cr. 65-1 y e) Cr. 65-2 (Stevenson et al., 1970).

La variabilidad de la estructura térmica es mostrada en la Fig. 31 en la que el Agua Tropical Superficial a fines de 1971 se halló en la capa de 30-40 m. Inmediatamente debajo se observó una marcada termoclina que se extendió de 35-50 m. Debajo de la termoclina la estratificación fue mínima y abarcó la capa de 50-250 m incluyendo isotermas de 14ºC y 13ºC. Este termostato parece ser debido al flujo de las aguas de la Corriente Subsuperficial Ecuatorial. Los cambios más notables fueron observados a partir de febrero-marzo de 1972, con la profundización de las isotermas de 13-20ºC. En agosto-septiembre 1973, las condiciones fueron similares a noviembre-diciembre 1971. Las figuras 32 y 33 muestran los grandes cambios de temperatura y salinidad de noviembre-diciembre 1971 a febrero-marzo 1972.

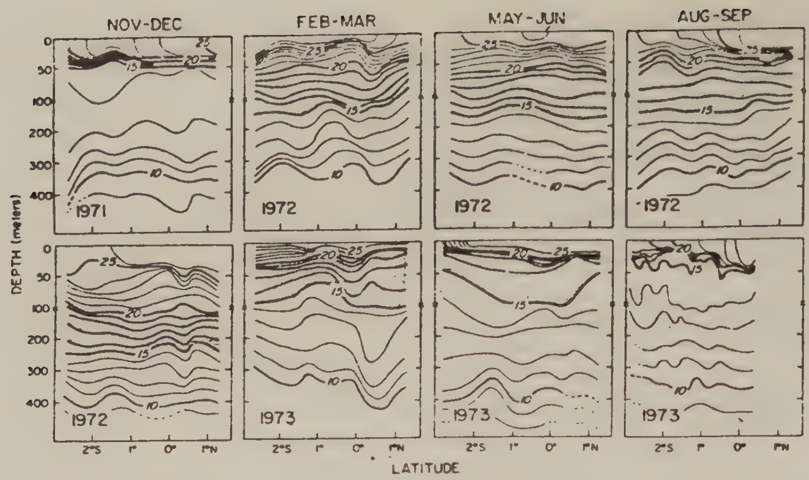


Fig. 31.- Secciones de temperatura a lo largo de 82-83°W frente a Ecuador en noviembre 1971 - septiembre 1973 (de Enfield, 1981).

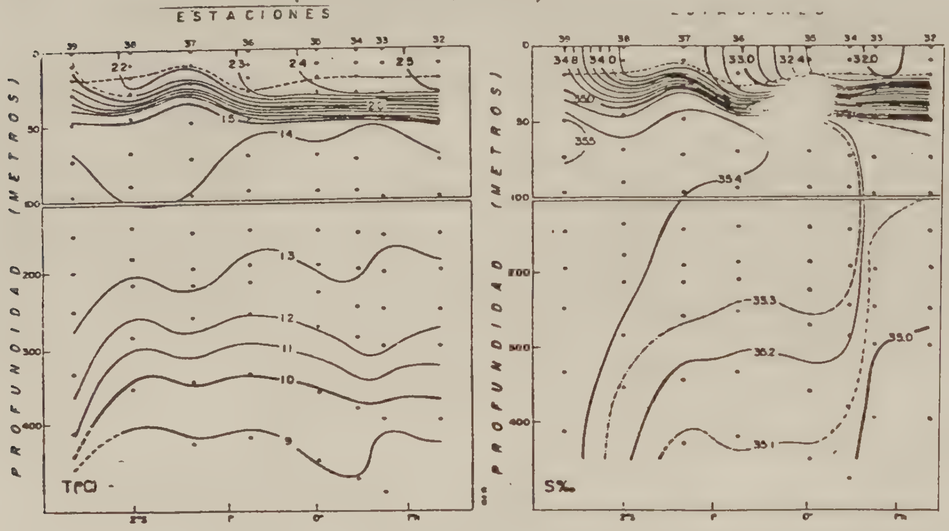


Fig. 32.- Secciones de temperatura y salinidad a lo largo de 82°30'W frente al Ecuador en noviembre-diciembre 1971 (de Enfield, 1976).

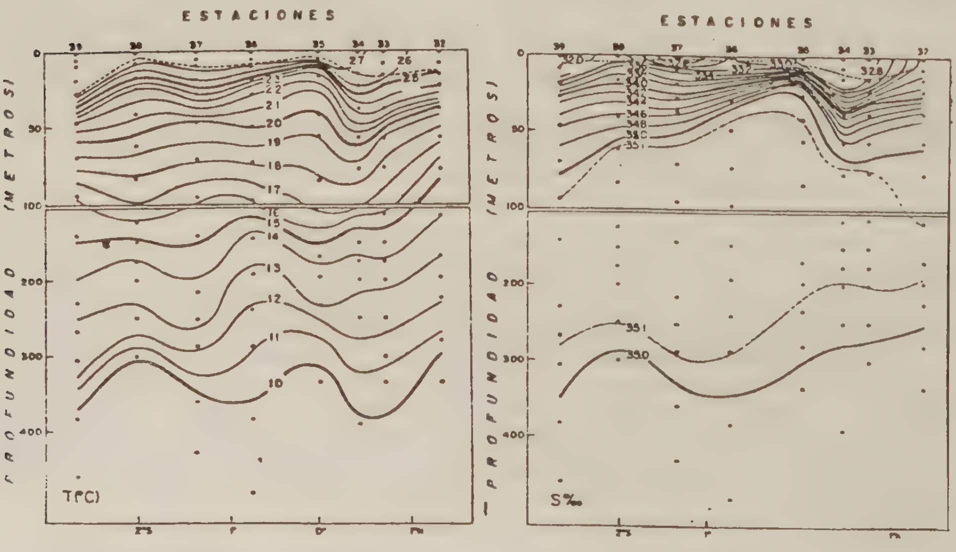


Fig. 33.- Secciones de temperatura y salinidad a lo largo de 82°30'W frente al Ecuador en febrero-marzo de 1972 (de Enfield, 1976).

En la sección frente a Cabo Blanco, la Corriente Peruana presenta a lo largo del Perú áreas de afloramiento, las cuales son identificadas por su baja temperatura, bajo contenido de oxígeno disuelto, y alto contenido de nutrientes. Las aguas que afloran pertenecen a la Corriente Subsuperficial Ecuatorial y son procedentes de los 50 a 75 m de profundidad. La velocidad del afloramiento a lo largo de la costa del Perú ha sido estimada aproximadamente en 1.9×10^{-5} cm/seg (Posner, 1957) y de $5\text{-}30 \times 10^{-5}$ cm/seg (Wyrtki, 1963).

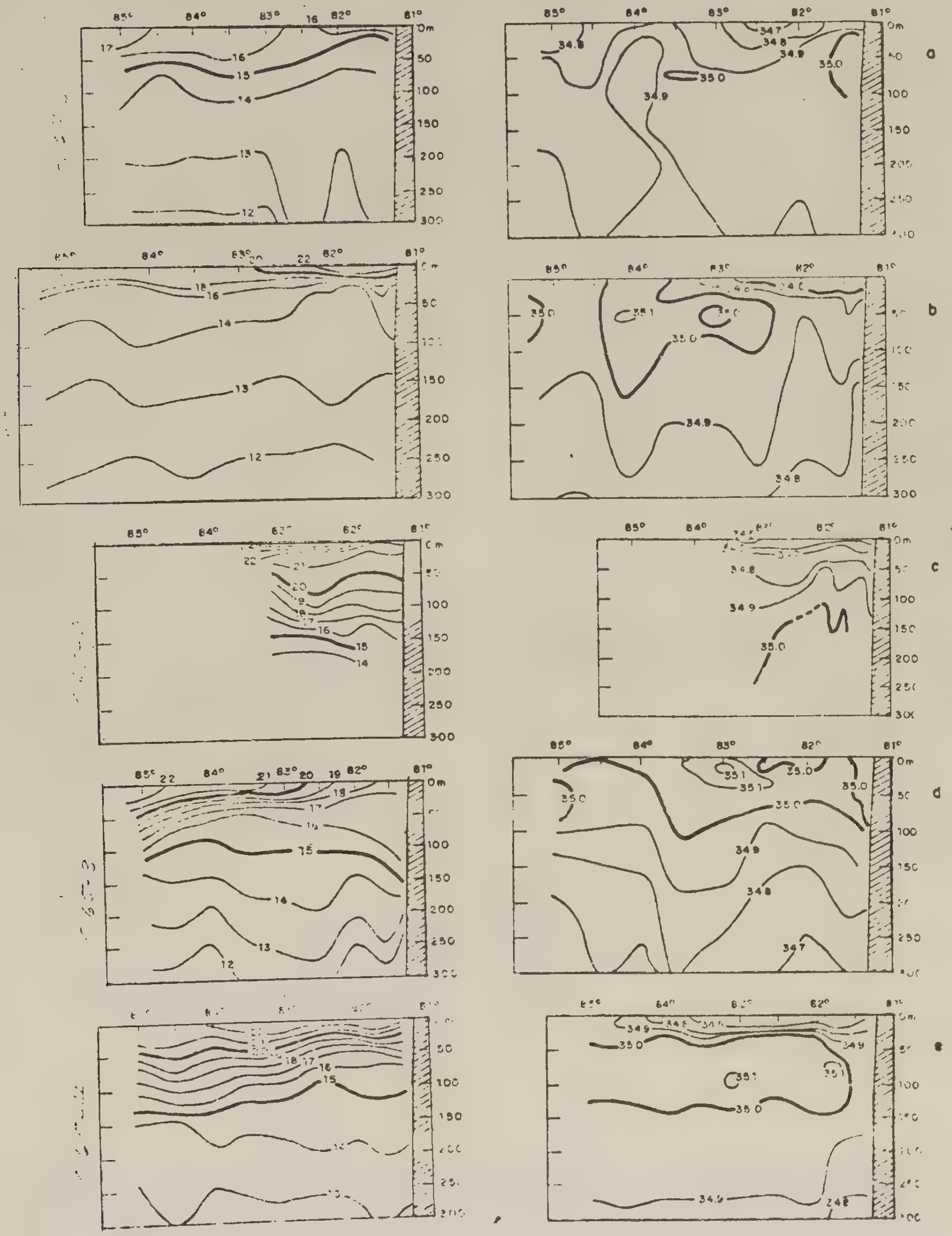


Fig. 34.- Secciones de temperatura y salinidad frente a Cabo Blanco: a) Cr. 64-3, b) Cr. 64-4, c) Cr. 65-2, d) Cr. 65-3 y e) Cr. 65-4 (de Stevenson *et al.*, 1970).

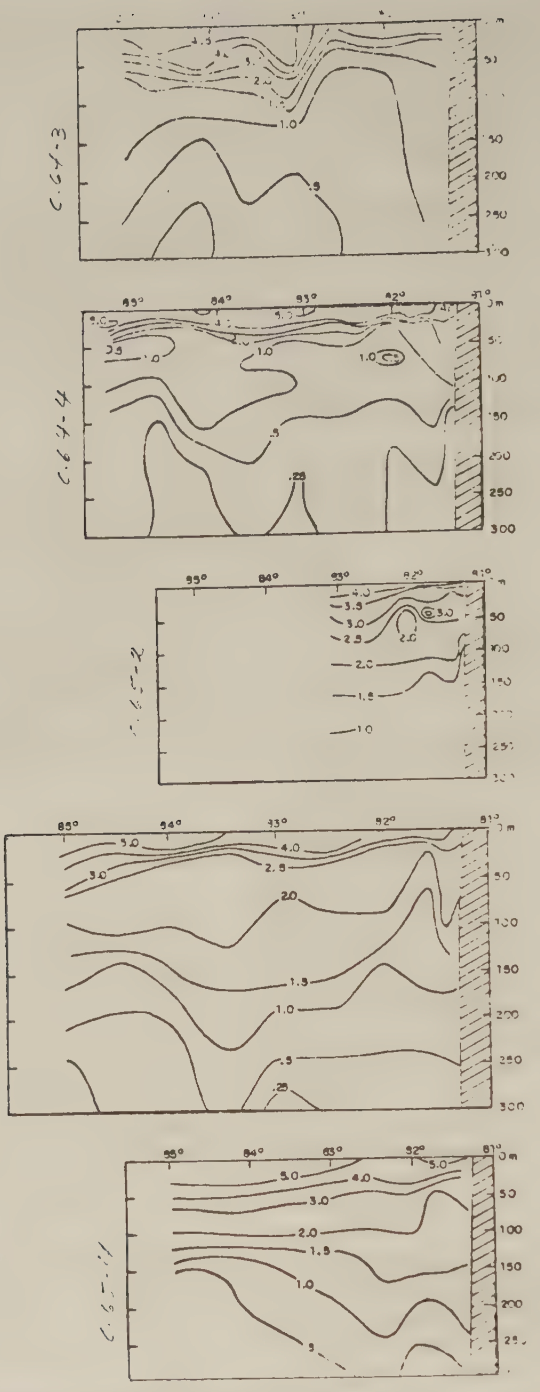


Fig. 35.- Secciones de oxīgeno disuelto frente a Cabo Blanco: a) Cr. 64-3, b) Cr. 64-4, c) Cr. 65-2, d) Cr. 65-3 y e) Cr. 65-4 (de Stevenson et al., 1970).

La distribucīōn durante El Niño 1965 (Figs. 34 y 35) es muy diferente a la del año frīo y al promedio, tanto en la temperatura como en la salinidad y oxīgeno disuelto.

En la secciōn frente a Arica se observa una celda de agua cālida, salina (Figs. 36 y 37) a unas 100 y 200 millas al oeste de Arica, la que es poco profunda. En el verano dicha celda puede trasladarse hacia la costa cuando los vientos meridionales cesan. En la distribuciōn vertical (Fig. 37) de la salinidad puede apreciarse la variabilidad de la Corriente Subsuperficial Perū-Chile que se caracteriza pos sus aguas mās salinas y menor contenido de oxīgeno disuelto (Fig. 38) cerca de la costa, entre los 50 y 300 m de profundidad, la cual varīa en extensiōn y profundīdad.

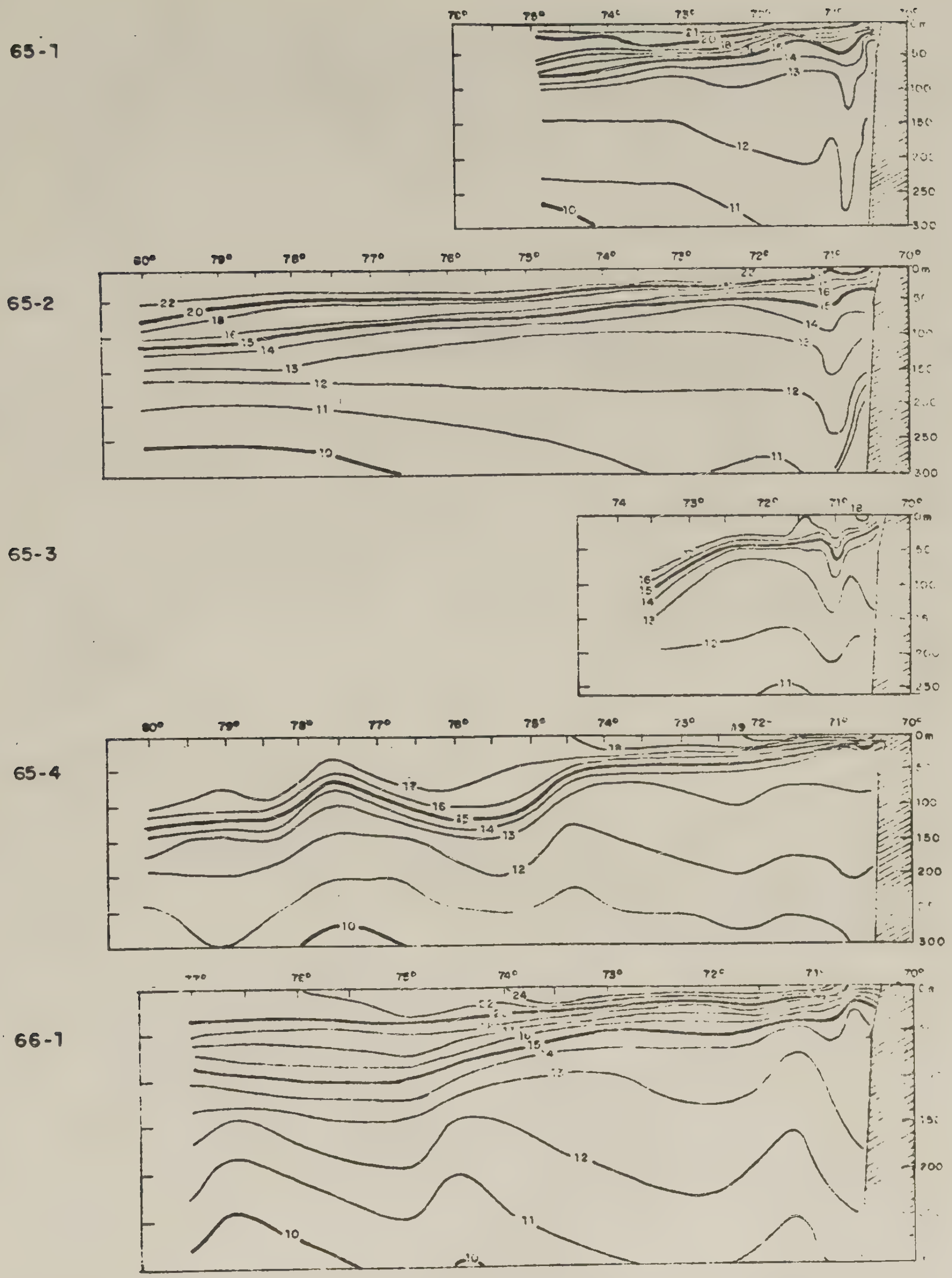


Fig. 36.- Secciones de temperatura frente a Arica: a) Cr. 65-1, b) 65-2, c) Cr. 65-3, d) Cr. 65-4 y e) Cr. 66-1 (de Stevenson *et al.*, 1970).

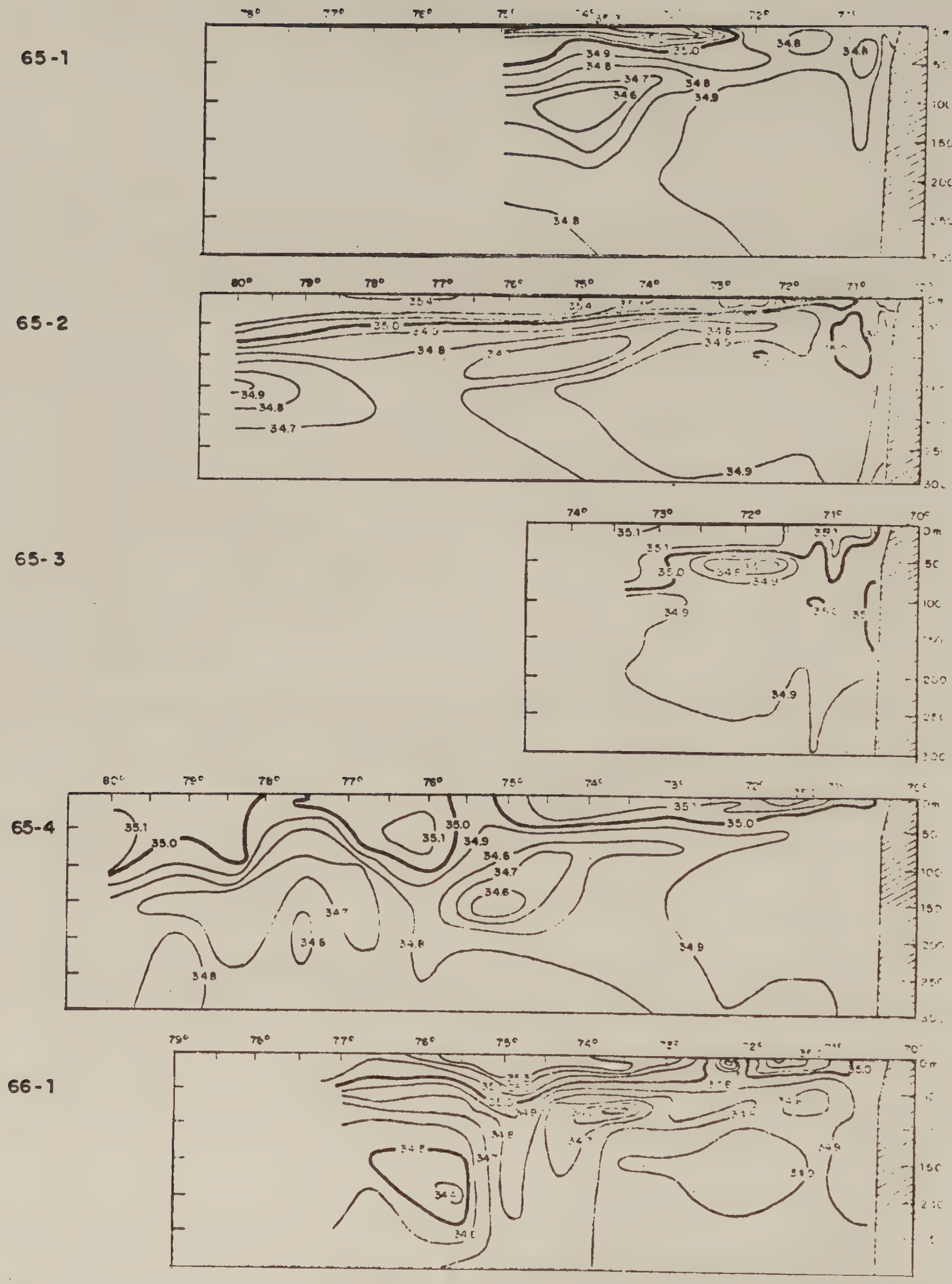


Fig. 37.- Secciones de salinidad frente a Arica: a) Cr. 65-1, b) Cr. 65-2 c) Cr. 65-3, d) Cr. 65-4 y e) Cr. 66-1 (de Stevenson *et al.*, 1970).

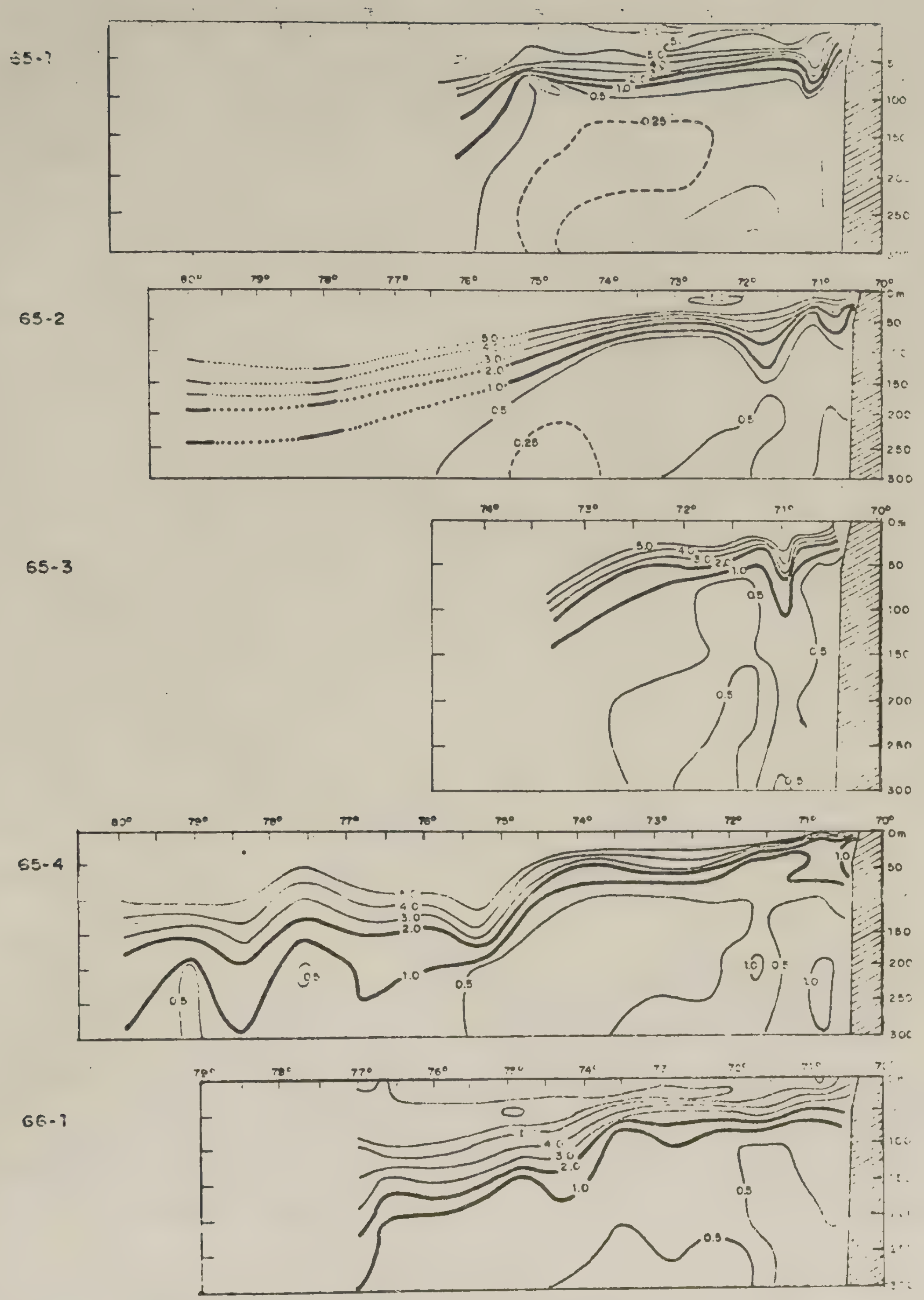


Fig. 38.- Secciones de oxígeno disuelto frente a Arica: a) Cr. 65-1, b) 65-2, c) Cr. 65-3, d) Cr. 65-4 y e) Cr. 66-1 (de Stevenson et al., 1970).

En la superficie del mar igualmente se observaron cambios estacionales y anuales de las condiciones oceanográficas; así, comparando las condiciones promedio de primavera y otoño con un año frío y años El Niño, se observan cambios en la distribución de la temperatura y salinidad, afectando la distribución y desarrollo de los organismos vivos.

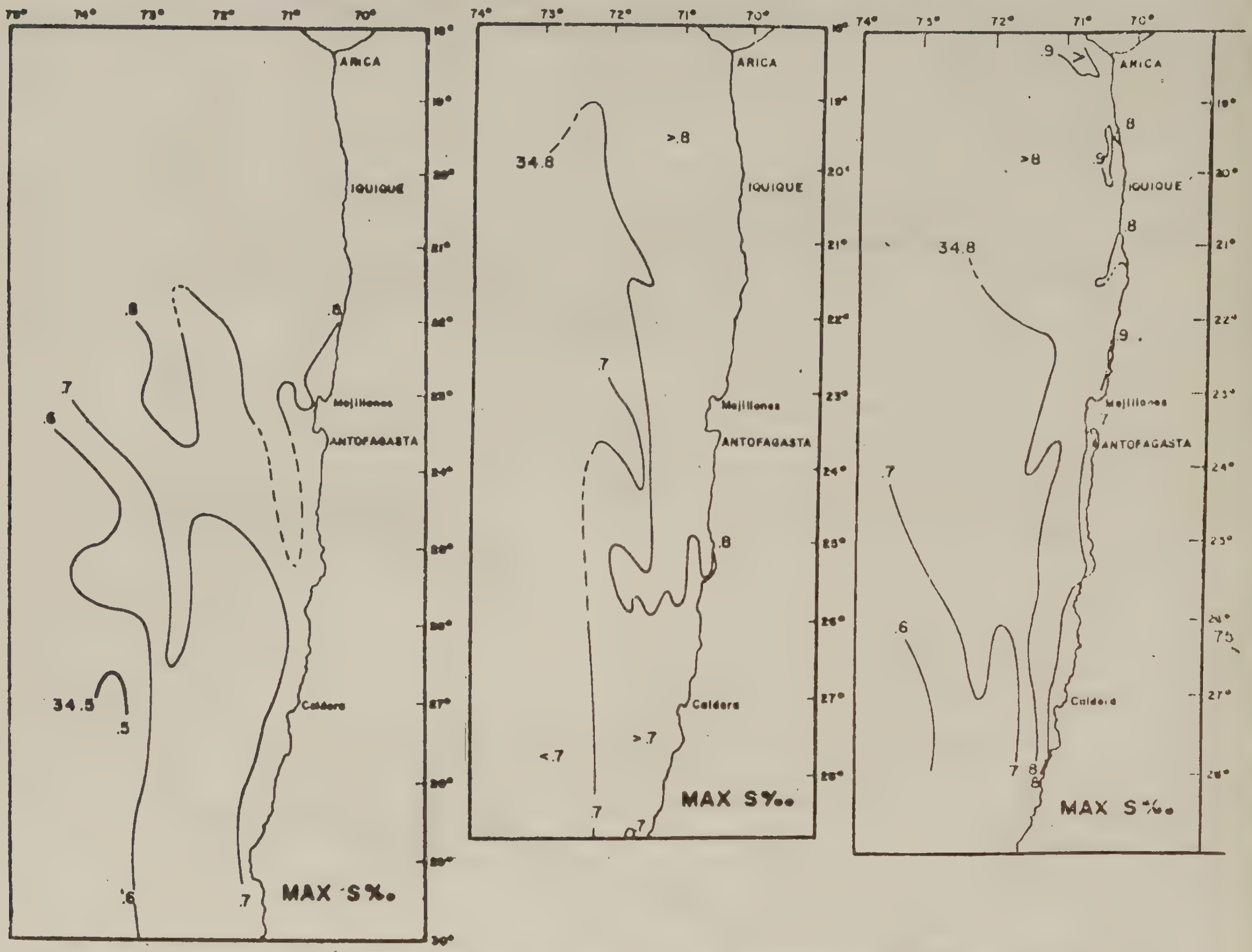


Fig. 39.- Distribución de la máxima de salinidad en el primavera de 1967 (a), 1971 (b) y 1972 (c) (de Robles et al., 1976).

Las variaciones anuales también pueden verse de la distribución de la máxima de salinidad (Fig. 39) de los años 1967, 1971 y 1972 (Robles et al., 1976).

VARIABILIDAD DEL MEDIO AMBIENTE Y SUS EFECTOS EN LA PRODUCTIVIDAD BIOLOGICA

Variabilidad del Medio Ambiente y sus Efectos en la Producción Primaria

La producción primaria depende de varios factores tales como: temperatura, radiación, nutrientes, procesos de circulación y de mezcla, pastoreo del zooplancton, hundimientos del fitoplancton, etc. Uno de los mecanismos más importantes para la fertilización de los océanos son los afloramientos, los cuales regulan la producción primaria.

Margalef (1978a, b) Vinogradov y Shuskina (1978), Walsh (1977) y Boje y Tomczak (1978) sostienen que los ecosistemas en los afloramientos son distintos de los ecosistemas marinos. Sin embargo, Cushing (1971 y 1978) señala que los ecosistemas de afloramiento costero no son ecosistemas distintos. Barber y Smith (1981) hacen una revisión completa de los ecosistemas de afloramiento costero y comparan las áreas de afloramiento de Oregon, Noroeste de Africa y Perú.

Blasco et al., (1980) y Smith et al. (1980), frente al Perú en 1976, hallaron cambios día a día en la composición del fitoplancton y zooplancton en una simple estación, debido en gran parte al transporte advectivo.

Las mayores concentraciones de clorofila "a" y producción se hallaron en las áreas de divergencia, de mezcla vertical y en la capa de mezcla superficial. La más alta producción (Owen y Zeitzschel, 1970; y Forsbergh y Joseph, 1963) se halló a lo largo de la costa peruana, debido al fuerte afloramiento (Fig. 40). La producción relativamente alta entre las Islas Galápagos y la costa fue debido al enriquecimiento de las aguas procedentes del afloramiento del norte del Perú.

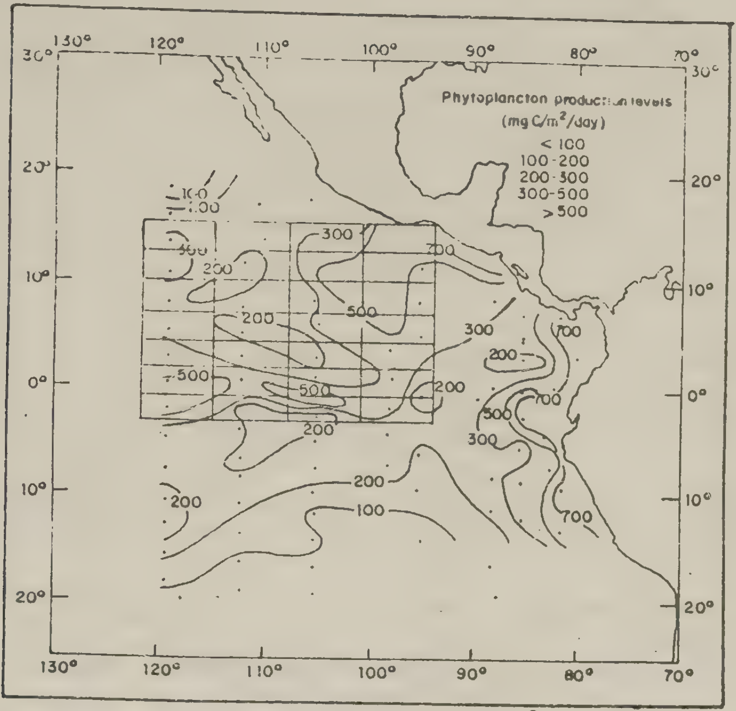


Fig. 40.- Producción primaria (mgC/m^2/día) en la capa eufótica de abril 1967 a marzo 1968 (de Owen y Zeitschel, 1970).

Frente a la costa de Chile el afloramiento costero es menor en comparación al Perú.

El afloramiento ecuatorial y la mezcla vertical explican la alta productividad cerca del Ecuador. Frente al Perú y Chile la producción varía estacionalmente de acuerdo a la calidad de las aguas afloradas y la intensidad y duración del afloramiento. La variabilidad del índice de productividad promedio frente a la costa peruana es mostrada en la Fig. 41, donde el mayor índice de productividad (>80 mg C/mg-Cl"a"/día) corresponde al área mayor de afloramiento. Frente al Perú afloran aguas de diferentes orígenes, dando por consiguiente, productividades diferentes; en algunos casos las aguas que afloran son procedentes de la Corriente Subsuperficial Ecuatorial que son más productivas que cuando afloran las aguas subantárticas. La variación de la isopigna de 25.8 (Guillén y Calienes, 1981) muestra la divergencia en años fríos y años El Niño durante el verano e invierno.

Por otro lado, se ha observado que no sólo los años El Niño afectan a la producción primaria sino también los años fríos (Guillén y Calienes, 1981), en el que a pesar del crecimiento intenso del fitoplancton, las aguas ricas en nutrientes contienen bajo contenido de células de fitoplancton debido a la inestabilidad de las aguas (Koblentz-Mishke, 1957), al rápido hundimiento de los organismos o probablemente al más intenso pastoreo del zooplancton. De la distribución de anomalías térmicas, se observa los años en que ha ocurrido El Niño (1965, 1969, 1972, 1976 y 1982-83) y los años fríos tales como: 1964, 1967-68, 1970-71 y 1974-75, lo que tiene un marcado efecto en la producción primaria; así, en El Niño débil de 1975 (Cowles et al., 1977) se observó en la región ecuatorial (Figs. 42 y 43) una producción primaria menor de 0.2 gC/m^2/día, equivalente a la

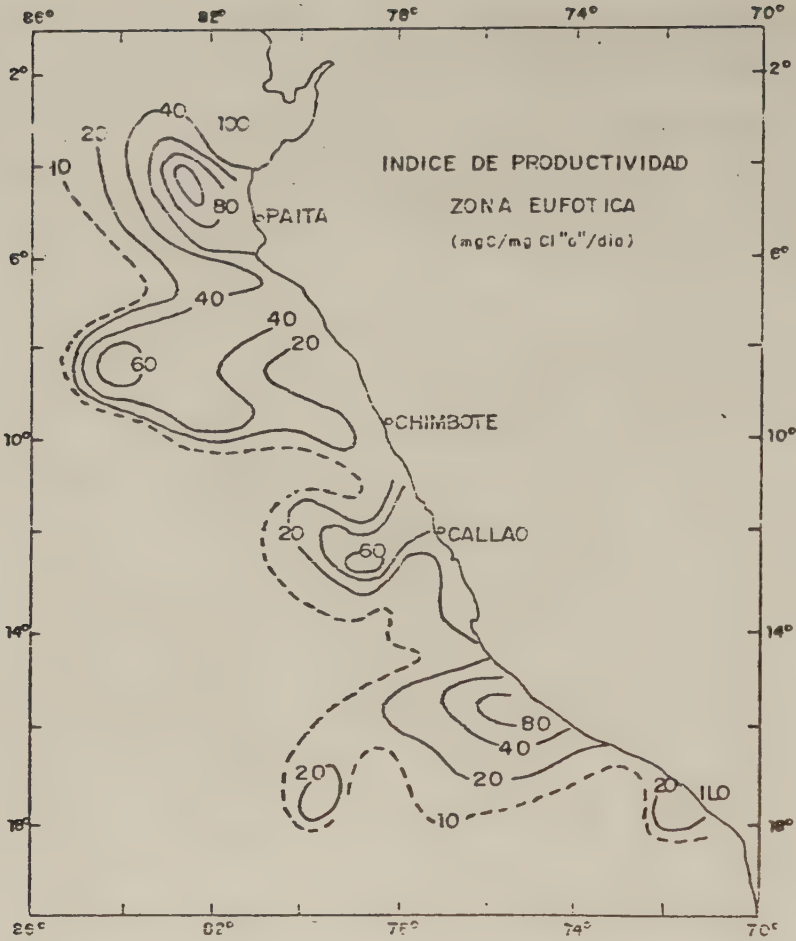

INDICE DE PRODUCTIVIDAD
ZONA EUFOTICA
(mgC/mg Cl "a"/dia)
PAITA
CHIMBOTE
CALLAO
ILO
86°
82°
78°
74°
70°
2°
6°
10°
14°
18°
10
20
40
60
80
100

Fig. 41.- Indice de productividad promedio (mg/mg cl "a"/día) frente al Perú.

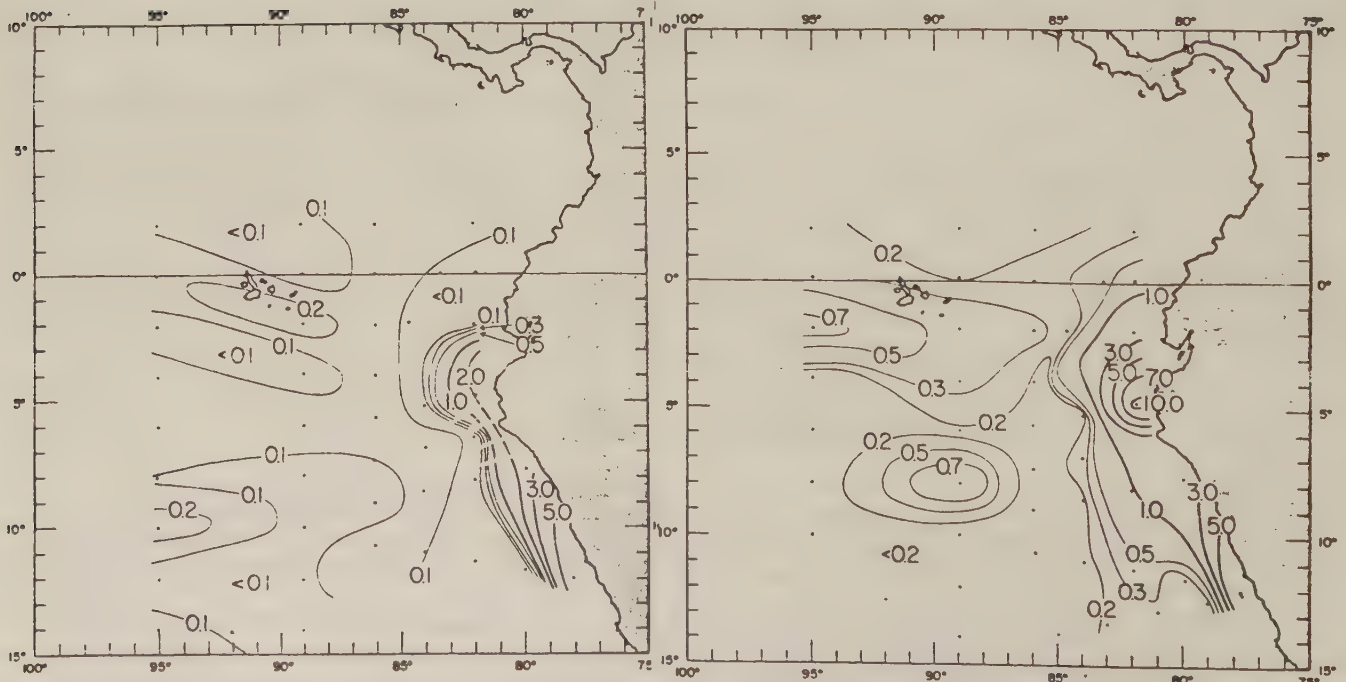

100°
95°
90°
85°
80°
75°
10°
5°
0°
5°
10°
15°
<0.1
0.1
0.2
0.3
0.5
1.0
2.0
3.0
5.0
<0.2
0.7
7.0
10.0

Fig. 42.- Distribución de la producción primaria (gC/m^2/día) en la capa eufótica en febrero-marzo y abril-mayo de 1975 (de Patzer *et al.*, 1978).

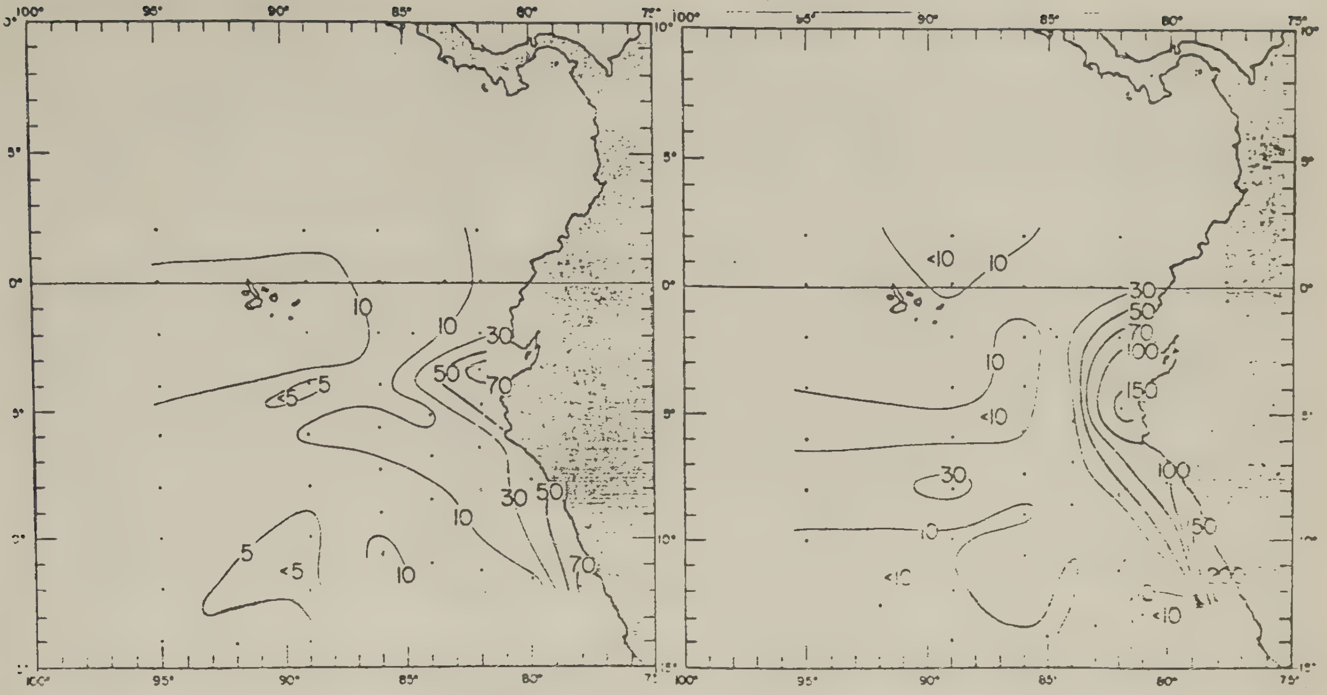


Fig. 43.- Distribución de la clorofila "a" (mg/m^2) en la capa eufótica en febrero-marzo y abril-mayo de 1975 (de Patzert et al., 1978).

quinta parte del promedio para el área. Los efectos biológicos de 1975 fueron cortos y no afectaron grandemente a la costa peruana. En cambio, en 1972 la producción primaria frente a las costas del Perú fue de 0.39 gC/m^2/día, un tercio de lo normalmente hallado (Guillén y Calienes, 1981). Los efectos de El Niño y de los años fríos (La Niña) se puede observar en la distribución de la clorofila "a" (Fig. 44) en el que durante los años 1965, 1969, 1972 y 1976, la concentración fue bajísima y muy inferior al año promedio de 1966. Igualmente, los años fríos se caracterizaron por sus bajísimas concentraciones de clorofila "a". Las figuras 45 y 46 presentan los cambios de producción primaria y clorofila "a" frente a Cabo Blanco, de marzo a mayo de 1975.

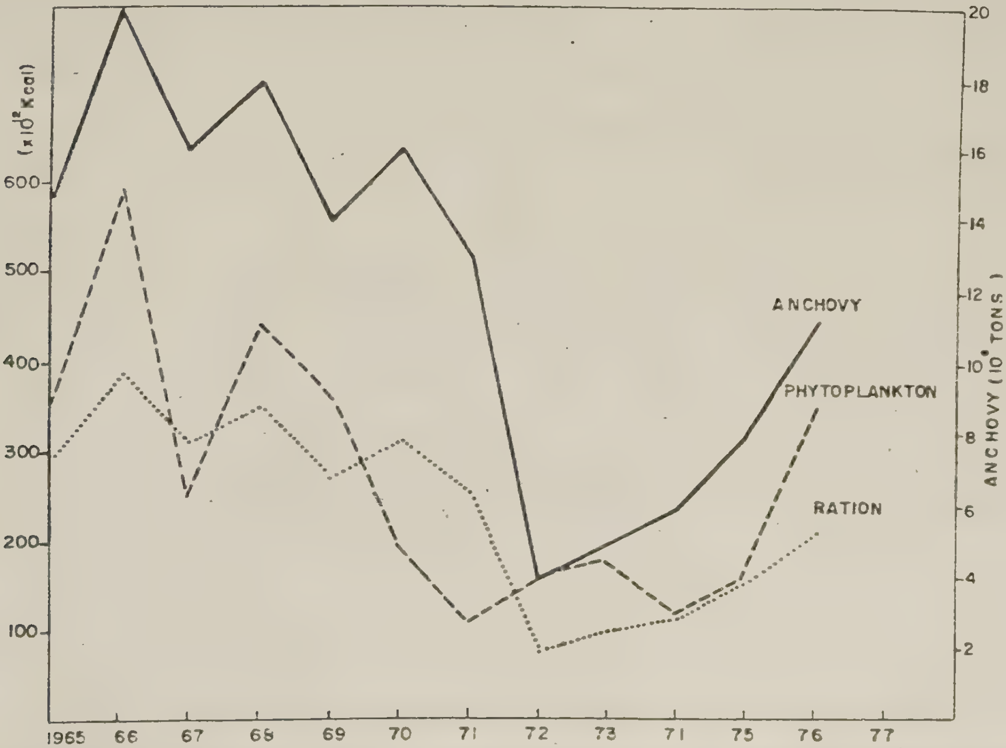


Fig. 44.- Biomasa de anchoveta (ton), fitoplancton (Kcal) y ración (Kcal) para el período 1965-77 (de Guillén y Calienes, 1981).

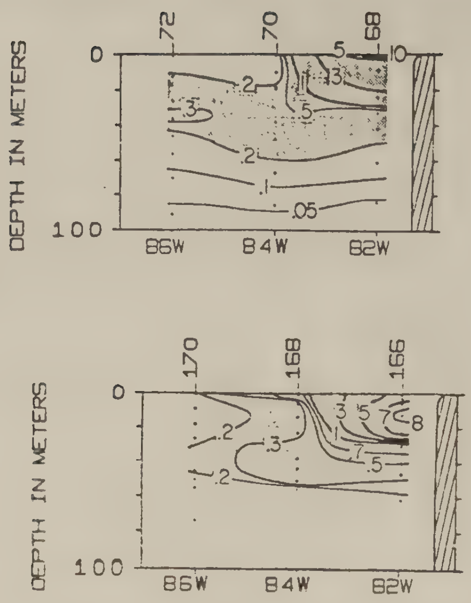


Fig. 45.- Secciones de clorofila "a" frente a Cabo Blanco en marzo y mayo de 1975 (de Patzert *et al.*, 1978).

La productividad depende en gran parte de la composición química de las masas de aguas (Calienes y Guillén, 1981). Las aguas más productivas corresponden a las aguas frías de la Corriente Peruana con valores mayores de 800 mg C/m^3/día en la superficie del mar, asociado con valores altos de nutrientes y clorofila "a" en la capa eufótica.

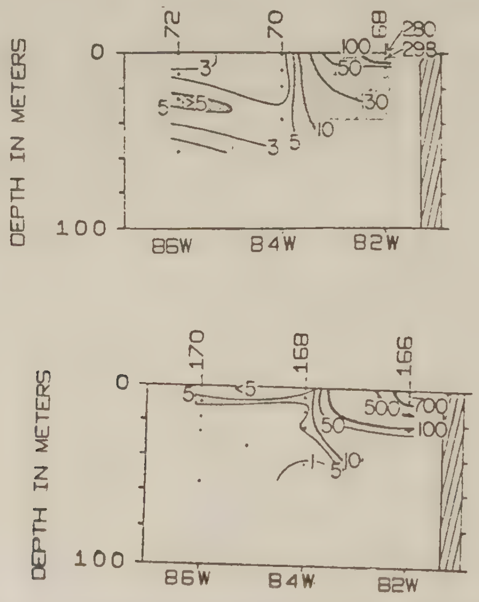


Fig. 46.- Secciones de producción primaria frente a Cabo Blanco en marzo y mayo de 1975 (de Patzert *et al.*, 1978).

Variabilidad del Medio Ambiente y sus Efectos en la Pesquería

Las capturas mundiales de los últimos tiempos han aumentado en forma espectacular de 19 millones de toneladas en 1950 a 61 millones de toneladas en 1980, y se espera un aumento en los años futuros debido al aumento de la tasa de crecimiento demográfico mundial. Por otro lado, el desarrollo de modernos instrumentos de pesca, nuevas técnicas de localización y de captura, de barcos pesqueros y el equipo de procesamiento del pescado han aumentado las capturas en los océanos.

Las fluctuaciones naturales y distribución de las plantas y animales en los océanos son comunes. Algunas fluctuaciones son bien correlacionadas con los cambios observados en el ambiente físico. Otras fluctuaciones naturales tales como el florecimiento de una marea roja o la desaparición de una gran población, tal como la sardina del Pacífico, no son obviamente correlacionadas a los cambios en el ambiente físico, cuyo nicho biológico fue llenado por la anchoveta del norte, y su población desde entonces ha permanecido baja. La variabilidad natural del ecosistema y la sobrepesca han sido las causas principales para la desastrosa caída de la población de la anchoveta peruana durante El Niño 1972.

La variabilidad del medio ambiente físico-químico no es el único factor que influye en la abundancia y la distribución de los recursos vivos, sino también los cambios de las actividades de pesca y las interacciones biológicas (Bakun et al., 1982).

Aún no se ha determinado cuáles son las variables ambientales más importantes en la variabilidad de las poblaciones de peces. Sin embargo, la distribución y abundancia de la mayoría de los recursos están relacionados directamente con la temperatura, alimentación y oxígeno, principalmente.

Los pelágicos presentan dos ambientes bien definidos: la zona nerítica que se caracteriza por sus aguas frías y su gran productividad, y la zona oceánica en la que predominan la Aguas Subtropicales Superficiales, que se caracterizan por sus aguas calientes y su baja productividad.

Alguna variabilidad puede ser también causada por cambios advectivos en la cantidad o clase de agua que es alimentada en la circulación costera por la Corriente Subsuperficial Perú-Chile, que fluye hacia el sur sobre la plataforma continental y en la parte superior del talud (Smith, 1978; Brockmann et al., 1980). Su core es bastante superficial sobre la plataforma continental y sus aguas afloran en la mayor parte de los afloramientos a lo largo de la costa peruana (Smith et al., 1971). En forma paralela, la Corriente Subsuperficial Ecuatorial podría tener una importancia en la influencia advectiva en el ecosistema ecuatorial.

Durante El Niño, las aguas de afloramiento son desplazadas por aguas calientes, pobres en nutrientes y productividad, causando un efecto negativo sobre los organismos vivos. El efecto adverso sobre la anchoveta no es bien conocido, pero sí afecta el desove y a las anchovetas juveniles.

La revisión de la captura de las principales especies por países de la región nos permite seguir las fluctuaciones relativas a años calientes y años fríos. Durante los eventos de El Niño, la captura de la anchoveta decrece mientras que otras especies tales como la sardina, jurel y caballa aumentaron notablemente en los siguientes años frente al Perú y Chile, debido a los grandes cambios oceanográficos. La calidad y cantidad del fitoplancton juegan también un papel muy importante como alimento para los siguientes niveles tróficos, ejemplo, la pesquería de anchoveta en el Perú durante 1972 y 1976 (Fig. 44). Como resultado de los cambios bruscos del ambiente durante los años fríos y calientes, se ha producido un cambio en la estructura del ecosistema marino, así como desplazamientos de ciertas especies, tal como lo ocurrido en el caso del desove de la sardina últimamente frente a las costas de Chile (Bernal, 1983), en el que se halló una nueva área de desove de *S. sagax* frente a Talcahuano y Golfo de Arauco. También se señala que los cambios interanuales de las variables biológicas no presentan una relación consistente con la ocurrencia de períodos fríos y cálidos; sin embargo, se observó una relación inversa entre la intensidad del desove de *E. ringens* y *S. sagax* y los períodos cálidos. Frente a las costas del Perú, los cambios oceanográficos tienen un pronunciado efecto en el desove de la anchoveta (Fig. 47).

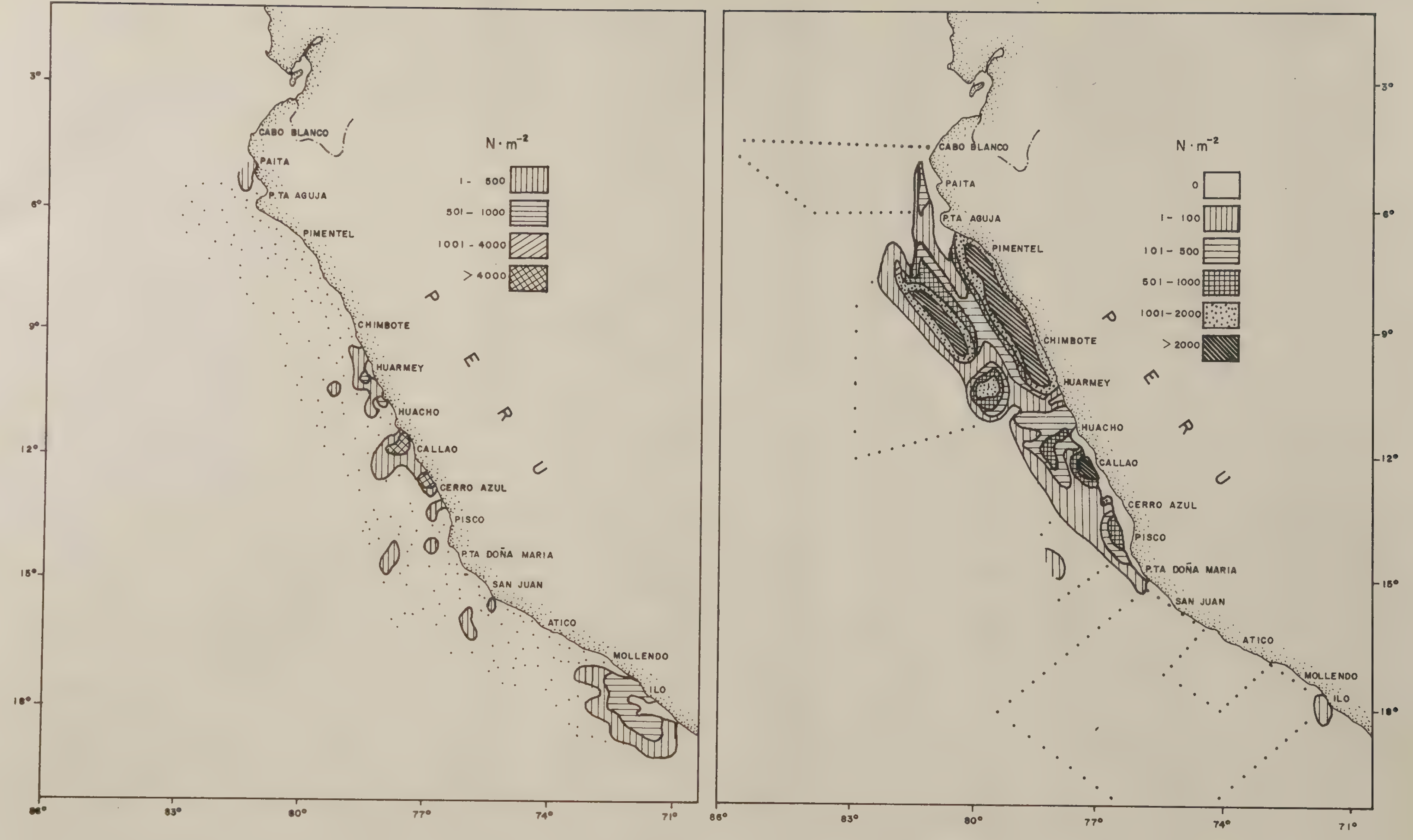

N·m^{-2}
1- 500
501- 1000
1001 - 4000
> 4000
CABO BLANCO
PAITA
P.TA AGUJA
PIMENTEL
CHIMBOTE
HUARMEY
HUACHO
CALLAO
CERRO AZUL
PISCO
P.TA DOÑA MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
P E R U
3°
6°
9°
12°
15°
18°
86°
83°
80°
77°
74°
71°
N·m^{-2}
0
1- 100
101- 500
501 - 1000
1001-2000
> 2000
CABO BLANCO
PAITA
P.TA AGUJA
PIMENTEL
CHIMBOTE
HUARMEY
HUACHO
CALLAO
CERRO AZUL
PISCO
P.TA DOÑA MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
P E R U
3°
6°
9°
12°
15°
18°
86°
83°
80°
77°
74°
71°

Fig. 47.- Distribución y abundancia de huevos de anchoveta en agosto 1967 y agosto 1972 (de Santander y de Castillo, 1979).

La distribución biogeográfica según ambientes ecológicos, son: 1) la Provincia Panamena, que abarca desde Bahía California, Colombia, Ecuador, hasta el extremo norte del Perú; 2) la Provincia desde Punta Aguja (06ºS) hasta la Isla Chiloé (42ºS); y 3) la Provincia Patagónica. También debe considerarse la Provincia Oceánica en el que predominan las Aguas Superficiales Subtropicales.

Durante los eventos de El Niño se encuentra a menudo especies de altura frente a la costa peruana y norte de Chile, tales como: el barrilete negro (*Auxis rochei*), el barrilete (*Katsuwonus pelamis*), el dorado (*Coryphaena hippurus*), sierra (*Scomberomorus maculatus*), peces voladores (*Exocoetus volitans*), el cangrejo nadador (*Euphylax dovii*), etc.

En Panamá, la más alta captura hasta 1977 correspondió a la anchoveta del Pacífico Central, con 165 mil toneladas en 1977; luego comenzó a decrecer hasta lograr valores de 4 mil toneladas en 1979. Le sigue las capturas del arenque de hebra o pinchagua, que a partir de 1972 se observó un aumento alcanzando una captura de 116 mil toneladas en 1979. Luego le sigue el atún, el barrilete y los camarones *Penaeus sp.*

En Colombia la mayor captura correspondió a los characidos, luego le siguen los silúridos, anchoveta del Pacífico Central y róbalos.

En Ecuador la mayor captura correspondió a la pinchagua, que a partir de 1972 aumentó su captura hasta lograr 575 mil toneladas en 1979; luego le siguen el atún y el barrilete. Sin embargo, la pesca tradicional y de importancia económica es la captura de camarones.

En el Perú, la captura de anchoveta ha declinado de 10.28 millones de toneladas en 1971 a 4.72 millones de toneladas en 1972, y luego ha continuado disminuyendo su captura. Las mayores capturas a partir de 1973 corresponden a la sardina, el jurel y la caballa con 1.17 millones, 68 y 42 mil toneladas, respectivamente, en 1981.

En Chile, la captura de la anchoveta en 1972 fue de 368 mil toneladas para luego decrecer, seguida por la sardina y el jurel con capturas de 1.5 y 866 mil toneladas en 1981. Las capturas de langostas, la cosecha de cholgas y algas en el sur son de importancia comercial.

El Niño de 1972-73 (Caviedes, 1981): Durante los meses de verano la temperatura superficial del mar a lo largo de la costa de Chile aumentó ligeramente sobre el promedio. El año de 1972 (Caviedes, 1981) fue considerado como un año anómalo por las condiciones oceánicas a lo largo de la costa durante el temprano invierno. En el invierno se observó un fuerte y ancho flujo de agua caliente en dirección sur entre las 100 y 150 millas de la costa, el cual causó un debilitamiento del afloramiento costero y una disminución del flujo costero hacia el norte.

En diciembre de 1972, la temperatura de las aguas frente a Arica, Antofagasta y Caldera estuvieron 2ºC arriba del promedio (Caviedes, 1981).

Las condiciones oceánicas anómalas en las aguas del norte de Chile no influyeron en el rendimiento de la pesquería pelágica sino hasta el invierno en 1972, y luego fue más pronunciado solamente en el verano de 1973. En enero de 1972 se capturó el 44% de toda la anchoveta capturada en 1972 (367 913 ton), mientras que en los tres meses de verano 1973, sólo se capturó anchoveta en un 30% de la captura correspondiente a 1973 (191 795 ton). La captura de las otras especies de aguas frías tales como la sardina, disminuyó; en cambio, la captura de peces de aguas tropicales, aumentaron.

Las anomalías oceánicas de 1975 no fueron tan pronunciadas como 1972-73 (Caviedes, 1981). En 1976 las condiciones oceanográficas al norte de Chile fueron restablecidas dando como resultado un alto rendimiento en la captura de pelágicos.

Rougiere y Chabanne (1983), comparando las variaciones de salinidad y el número o peso de la captura de la atún, hallaron que el período de baja salinidad correlaciona muy bien con las grandes capturas de atún, con un coeficiente de correlación para el período 1976-82 de -0.56. Sin embargo, considerando sólo los períodos cuando la salinidad es inferior a 35.5 o/oo y arriba de 36.0 o/oo, el coeficiente de correlación fue de -0.82, indicando que hay una fuerte correlación entre la salinidad de las aguas superficiales y la tasa de captura de atún.

REFERENCIAS

Alarcón, E. 1975. Oceanographic conditions in coastal waters off Coquimbo. International Symposium Coastal Upwelling Proceedings. Coquimbo, Chile, November 18-19. Fundación Chile: 149-161.

Alarcón, E. y J. Pineda. 1969. Descripción oceanográfica estacional de las aguas frente a Valparaíso. Bol.Cient.IFOP, Chile. 11-31 p.

Austin, T.S. 1958. Variations with depth of oceanographic properties along the equator in the Pacific. Trans.Am.Geoph.Union. 39(6):1055-1063.

Bakun, A., J. Beyer, D. Pauly, J.G. Pope y G.D. Sharp. 1982. Ocean sciences in relation to living resources. Can.J.Fish Aquat.Sci. 39:1059-1070.

Basten, J. 1978. Oceanografía de las aguas costeras del norte de Chile. Resultados del Crucero de Otoño de 1975 (mayo). Rev.Com.Perm.Pacífico Sur. 9:83-102.

Bennett, E.B. 1963. An oceanographic atlas of the eastern tropical Pacific Ocean based on data from EASTROPIC EXPEDITION, October-December 1955. Bull.Inter-Amer.Trop.Tuna Comm. 8(2):33-165.

____________. 1965. Currents observed in Panama Bay during September-October 1958. Bull.Inter-Amer.Trop.Tuna Comm. 10(7):399-457.

____________. 1966. Monthly charts of surface salinity in the eastern tropical Pacific Ocean. Bull.Inter-Amer.Trop.Tuna Comm. 11(1):3-44.

Barber, R.T. y R. Smith. 1981. Coastal upwelling ecosystems. pp. 31-68. In Analysis of marine ecosystems (A.R. Longhurst, ed.). Academic Press, New York, San Francisco.

Bernal, P. 1983. (MS). Variabilidad biológica interanual en la Corriente de California y en la región meridional del Pacífico Sureste. Presentado a la Tercera Reunión del Grupo de Trabajo Conjunto COI/OMM/CPPS sobre Investigaciones de "El Niño". 47 p.

Blasco, D., M. Estrada y B. Jones. 1980. Phytoplankton distribution and composition in the Northwest Africa upwelling region near Cabo Corbeiro. Deep-Sea Res.

Boje, R. y M. Tomczak. 1978. Ecosystem analysis and the definition of boundaries in upwelling regions. pp. 3-11. In Upwelling ecosystems (R. Boje and M. Tomczak, eds). Springer-Verlag, New York.

Brandhorst, W. 1963. Descripción de las condiciones oceanográficas en las aguas costeras entre Valparaíso y el Golfo de Arauco, con especial referencia al contenido de oxígeno y su relación con la pesca. Min.Agri.Chile. 1-55.

____________. 1971. Condiciones oceanográficas estivales frente a la costa de Chile. Depto. de Oceanología, U. de Chile, Valparaíso, Chile. Rev.Biol.Mar. 14(3):1-20.

Brandhorst, W. y R. Cañón. 1967. Resultados oceanográfico-pesqueros aéreos en el norte de Chile. Pub.IFOP, Chile. 29:44 p.

Brandhorst, W. y O. Rojas. 1967. Investigaciones sobre los recursos de la anchoveta y sus relaciones con las condiciones oceanográficas en agosto-setiembre de 1963 y marzo-junio de 1964. Pub.IFOP, Chile. 31:17 p.

____________. 1968. Investigaciones sobre los recursos de la anchoveta y sus relaciones con las condiciones oceanográficas en agosto a octubre de 1964. Pub.IFOP, Chile. 36:17 p.

Brockmann, C., E. Fahrabach, A. Huyer y R.L. Smith. 1980. The poleward undercurrent along the Peru coast, 5°-15°S. Deep-Sea Res. 27A:847-856.

Calienes, R. y O. Guillén. 1981. Masas de agua y producción primaria en el Perú. Bol.Inst.Mar Perú-Callao. Volumen Extraordinario, ICANE, 155-163.

Caviedes, C.N. 1981. The impact of El Niño on the development of the Chilean fisheries. pp. 351-368. In Resource management and environmental uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley Interscience, New York.

Cochrane, J.D. y S. Zuta. 1968. (MS). Equatorial currents east of the Galapagos Islands in February-March, 1967. Texas A & M University, Department of Oceanography.

Cowles, T.J., R.T. Barber y O. Guillén. 1977. Biological consequences of the 1975 El Niño. Science. 195:285-287.

Cushing, D.H. 1971. A comparison of production in temperate seas and upwelling areas. Trans.Roy. Soc.South Africa. 40:17-33.

___________. 1978. Upper trophic level in upwelling areas. pp. 101-110. In Upwelling ecosystems (R. Boje and M. Tomczak, eds). Springer-Verlag. New York.

Enfield, O. 1976. Oceanografía de la región norte del frente ecuatorial aspectos físicos. Reunión de Trabajo sobre el fenómeno conocido como "El Niño". Guayaquil, Ecuador, 4-12 de diciembre de 1974. FAO Inf.Pesca. (185):299-334.

Forsbergh, E. 1963. Some relationship of meteorological hydrographic and biological variables in the Gulf of Panama. Bull.Inter-Amer.Trop.Tuna Comm. 7(1):1-109.

___________. 1969. On the climatology, oceanography and fisheries of the Panama Bight. Bull. Inter-Amer.Trop.Tuna Comm. 14(2):49-365.

Forsbergh, E. y W.N. Broenkow. 1965. Observaciones oceanográficas del Océano Pacífico Oriental recolectadas por el barco Shoyo Maru, octubre 1963 - marzo 1964. Bull.Inter-Amer.Trop.Tuna Comm. 10(2):84-237.

Forsbergh, E. y J. Joseph. 1963. Phytoplankton production in the South-Eastern Pacific. Nature. 200(4901):87-88.

Guillén, O. 1967. Anomalies in the water off the Peruvian coast during March and April 1965. Stud.Trop.Oceanogr.Miami. 5:452-465.

___________. 1971. The "El Niño" phenomenon in 1965 and its relations with the productivity in coastal Peruvian waters. pp. 187-196. In Fertility of the sea (J. Costlow, ed.). Gordon and Breach, New York.

___________. 1973. Carbon/chlorophyll relationships in Peruvian coastal waters. pp. 373-385. In Oceanography of the South Pacific 1972 (compiled by R. Fraser). Wellington, New Zealand National Commission for UNESCO.

___________. 1976. El sistema de la Corriente Peruana. Parte I: Aspectos físicos. Reunión de Trabajo sobre el fenómeno conocido como "En Niño". Guayaquil, Ecuador, 4-12 de diciembre de 1974. FAO Inf.Pesca. (185):243-284.

Guillén, O. y R. Calienes. 1981. Biological productivity and El Niño. pp. 255-282. In Resource management and environmental uncertainty: lessons from coastal upwelling fisheries (M.H. Glatz and J.D. Thompson, eds). Wiley Interscience, New York.

Gunther, E.R. 1936. A report on oceanographical investigation in the Peru coastal currents. Discovery Rep. 13:107-276.

Inostroza, H. 1972. Atlas oceanográfico de Chile. Instituto Hidrográfico de la Armada, Pub.3041, Valparaíso, Chile. 171 p.

___________. 1973. Some oceanographic features of northern Chilean waters in July 1962. pp. 37-46. In Oceanography of the South Pacific (compiled by R. Fraser). Wellington, New Zealand National Commission for UNESCO.

Jones, H.J. 1973. Vertical mixing in the Equatorial Undercurrent. J.Phys.Oceanogr. 3(3):286-296.

Knauss, J.A. 1960. Measurements of the Cromwell Current. Deep-Sea Res. 4:265-286.

____________. 1966. Further measurements and observations on the Cromwell Current. J.Mar.Res. 24:205-240.

Koblentz-Miske, O.I. 1957. On phytoplankton production in the western north Pacific Ocean in spring, 1955. Doklady Acad.Sci.USSR. 116:1029-1031.

Love, C. (ed.). 1970-77. Eastropic Atlas. Circ.NOAA/NMFS. (33) Vol.I al II.

Margalef, R. 1978a. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1:493-509.

____________. 1978b. What is an upwelling ecosystem? pp. 12-14. In Upwelling ecosystems (R. Boje and M. Tomczak, eds). Springer-Verlag, New York.

Mujica, R. 1972. Oceanografía del mar peruano en Historia Marítima del Perú. Talleres Gráficos, Perú. 1:221-474.

Owen, R.W. y B. Zeitzchel. 1970. Phytoplankton production: seasonal change in the Oceanic Eastern Tropical Pacific. pp. 32-36. In Marine Biology International Journal on Life in Oceans and Coastal Waters. Springer-Verlag, Germany.

Posner, G.S. 1957. The Peru current. Bull.Bingham.Oceanogr.Collect. 16(2):106-155.

Parra, R. 1977. Resultados oceanográficos del Pacífico colombiano durante el año de 1976. Boletín Científico Armada Nacional Cartagena, Colombia. 1(1):41 p.

Reid, J.L. 1959. Evidence of a South Equatorial Countercurrent in the Pacific Ocean. Nature 184(4681):209-210.

____________. 1961. On the geostrophic flow at the surface of the Pacific Ocean with respect to the 1000 decibar surface. Tellus. 13(4):489-502.

____________. 1962. On circulation phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol.Oceanogr. 7:237-306.

Robles, F. 1966. Graphical description of oceanographic conditions off Tarapaca Province, based upon data from Marchile II Expedition. Instituto Hidrográfico de la Armada. Valparaíso, Chile. 29 p.

____________. 1968. Descripción general de las condiciones oceanográficas en aguas chilenas. Sinópsis sobre algunos aspectos de las pesquerías chilenas. Valparaíso, Chile.

Robles, F., E. Alarcón y A. Ullao. 1976. Las masas de agua en la región norte de Chile y sus variaciones en un período frío (1967) y en períodos cálidos (1969, 1971-1973). Reunión de Trabajo sobre el fenómeno conocido como "El Niño". Guayaquil, Ecuador, 4-12 de diciembre de 1974. FAO Inf.Pesca. (185)94-196.

Rougerie, F. y J. Chabanne. 1983. Relationship between tuna and salinity in Tahitian coastal waters. Tropical Ocean-atmosphere Newsletter. 17:12-13.

Santander, H. y O.S. de Castillo. 1979. El ictioplancton de la costa peruana. Bol.Inst.Mar Perú-Callao. 4(3):72-111.

Schaefer, M., Y.M. Bishop y C.V. Howard. 1958. Some aspects of upwelling on the Gulf of Panama. Bull.Inter-Amer.Trop.Tuna Comm. 3(2):79-131.

Sievers, H.A. y N. Silva. 1973. Variaciones estacionales de temperatura, salinidad y contenido de oxígeno frente a la Bahía de Valparaíso (mayo de 1963 - abril de 1969). Inv.Mar. 4(1):1-16.

____________. 1976. Masas de agua y circulación en el Océano Pacífico Sudoriental. Latitudes 18ºS 33ºS (Operación Oceanográfica Marchile VII). Reunión de Trabajo sobre el fenómeno conocido como "El Niño". Guayaquil, Ecuador, 4-12 diciembre de 1974. FAO Inf.Pesca. (185):197-231.

Silva, N. 1973. Variaciones estacionales de temperatura, salinidad y contenido de oxígeno en la zona costera de Valparaíso (setiembre de 1969 - agosto de 1970). Inv.Mar. 4(3):89-112.

Smith, R., D. Enfield, T.S. Hopkins y R.D. Pillsburg. 1971. La circulación en un sistema de afloramiento: Campaña Pisco. Inv.Pesq. 35(1):9-24.

Smith, R.L. 1978. Poleward propagating perturbations in currents and sea levels along the Peru coast. J.Geophys.Res. 83:6083-6092.

Smith, S.L., K.H. Brink, H. Santander, T.J. Cowles y A. Huyer. 1980. The effect of advection on variations in zooplankton at a single location near Cabo Nazca, Peru. pp. 400-410. In Coastal upwelling research, 1980 (F.A. Richards, ed.). American Geophysical Union, Washington, D.C.

Stevenson, N.M. 1970. Circulation in the Panama Bight. J.Geoph.Res. 75(3):659-672.

Stevenson, N., O. Guillén y J. Santoro. 1970. Marine atlas of the Pacific coastal waters of South America. Univ.Calif.Press. 23 pp. plus charts.

Stevenson, M. y B. Taft. 1971. New evidence of the Equatorial Undercurrent, east of the Galapagos Islands. J.Mar.Res. 20(2):103-115.

Sverdrup, H.V., M.W. Johnson y R.H. Fleming. 1946. The oceans, their physics, chemistry and general biology. New York, Prentice-Hall. 1087 p.

Thomas, W.H. 1966. Surface nitrogenous nutrients and phytoplankton in the northeastern tropical Pacific Ocean. Limnol.Oceanogr. 11:393-400.

Tsuchiya, M. 1968. Upper waters and circulation of the intertropical Pacific Ocean. Johns Hopkins Oceanogr.Stud. 4:50 p.

Vinogradov, M.E. y E.A. Shushkina. 1978. Some development patterns of plankton communities in the upwelling areas of the Pacific Ocean. Mar.Biol. 48:357-366.

Walsh, J.J. 1978. The biological consequences of interaction of the climatic El Niño, and event scales of variability in the eastern tropical Pacific. Rapp.P.-v.Réun.Cons.Int.Explor.Mer. 173:182-192.

White, W.B. 1969. The Equatorial Undercurrent, the South Equatorial Countercurrent and their extension in the South Pacific Ocean, east of the Galapagos Islands during February-March, 1967. Texas A and M University Ref. 69-4-T, 74 p.

Wooster, W.S. 1952. Shellback Expedition 17 May to 27 August 1952. Scripps.Tech.Rep.Scripps Inst.Oceanogr. (SIO Ref. 52-63), 14 p.

____________. 1959. Oceanographic observations in the Panama Bight, Askoy Expedition, 1941. Amer.Mus.Nat.Hist.Bull. 118(3):117-151.

____________. 1960. "El Niño". Rep.CalCOFI. (7):43-45.

____________. 1961. Further evidence of a Pacific South Equatorial Countercurrent. Deep-Sea Res. 8(3/4):294-297.

____________. 1969. Equatorial front between Peru and Galapagos. Deep-Sea Res. 16 Suppl:407-419.

____________. 1970. Eastern boundary currents in the South Pacific. Scientific Exploration of the South Pacific. National Academy of Sciences, Washington D.C. 60-68.

Wooster, W.S. y T. Cronwell. 1958. An oceanographic description of the eastern tropical Pacific. Bull.Scripps Inst.Oceanogr. 7(3):169-281.

Wooster, W.S. y M. Gilmartin. 1961. The Peru-Chile Undercurrent. J.Mar.Res. Vol. 1963, Bingham Oc. Lab. Yale University.

Wooster, W.S. y J.L. Reid. 1963. Eastern boundary currents. In The sea (M.N. Hill, ed.). New York, Vol. 2:253-280.

Wooster, W.S., T.J. Chow y I. Barrett. 1965. Nitrite distribution in Peru waters. J.Mar.Res. 23(3):210-221.

Wooster, W.S. y O. Guillén. 1974. Características de "El Niño" en 1972. Bol.Inst.Mar Perú-Callao. 3(2):44-71.

Wyrtki, K. 1963. The horizontal and vertical field of motion in the Peru Current. Bull.Scripps Inst.Oceanogr. 8(4):313-346.

____________. 1964. The thermal structure of the eastern Pacific Ocean. Dt.Hydrogr.Z., Erganzungsheft, Ab. 84 p.

____________. 1965. Surface currents of the eastern tropical Pacific Ocean. Bull.Inter-Amer.Trop. Tuna Comm. 9:271-304.

____________. 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr.Mar.Biol. Ann.Rev. 4:33-68.

____________. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Inst.J. Oceanol. and Limnol. 1(2):117-147.

Wyrtki, K., E. Stroup, W. Patzert, R. William y N. Quinn. 1976. Predicting and observing El Niño. Science. 191:343-346.

Zuta, S. y O. Guillén. 1970. Oceanografía de las aguas costeras del Perú. Bol.Inst.Mar Perú-Callao. 2(5):161-223.

Zuta, S. y W. Urquizo. 1972. Temperatura promedio de la superficie del mar frente a la costa peruana, período 1928-1969. Bol.Inst.Mar Perú-Callao. 2(8):462-519.

Zuta, S., D. Enfield, J. Valdivia, P. Lagos y C. Blandin. 1976. Aspectos físicos del fenómeno "El Niño" 1972-73. Reunión de Trabajo sobre el fenómeno conocido como "El Niño". Guayaquil, Ecuador, 4-12 de diciembre de 1974. FAO Inf.Pesca. (185):3-61.

Zuta, S. y O. Guillén. 1983. (MS). Informe del avance del Programa Oceanográfico del ERFEN en el Perú en 1981-82. Tercera Reunión de Trabajo del Comité Científico del ERFEN. Cali, Colombia, 12 p.

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

PHYSICS AND FISH POPULATIONS: SHELF SEA FRONTS AND FISHERIES

by

J.R. Hunter[1] and Gary D. Sharp[2]

[1] Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service
NOAA, P.O. Box 271
La Jolla, CA 92038
USA

[2] Fishery Resources and Environment Division
Fisheries Department
FAO, Via delle Terme di Caracalla
00100 Rome, Italy

Resumen

Entre los problemas de proyectar la producción de la pesca están la gran cantidad de variables complejas, dentro de las cuales la producción primaria y los procesos físicos que promueven esta produeción tienen gran importancia. Se revisa una vez más la importancia de las escalas de tiempo y espacio en relación a varios procesos biológicos de importancia relacionados con la pesca, y se describe una clase especial de fenómeno físico y sus características.

Los frentes marinos en la plataforma derivan de numerosos procesos: frentes en la interrupción de la plataforma; frentes costeros; corrientes sobre la plataforma impulsados por el viento; frentes causados por las mareas. Estos se describen en suficiente detalle como para que sus mecanismos puedan ser comparados, y se describen las características de los frentes marinos de la plataforma. Estos son procesos determinados por las estaciones y la geografía.

Los requerimientos para que se forme un frente son de dos tipos:

a) Debe haber suficiente energía (del viento o las mareas) para formar un área de mezcla, con una región adyacente donde el grado de mezcla, con una región adyacente donde el grado de mezcla es menor y pueda ocurrir estratificación.

b) Para que ocurra la estratificación debe haber una fuerte presión o empuje hacia arriba del fluido ya sea por el incremento de la densidad de los estratos más profundos o una disminución de la densidad de las capas superiores, por ejemplo lluvia o pérdida de calor.

Si se tiene información sobre la observación de energía y los procesos de estratificación es posible hacer una serie de prediciones sobre dónde se pueden generar los frentes marinos en la plataforma. Las principales áreas de plataforma continental de los océanos del mundo se han ordenado para mostrar las regiones potenciales para la formación de frentes inducidos por mareas. Estos parecerían ser útiles para relacionar con áreas de producción de peces pelagícos-neríticos, tal como fuera sugerido por Illes y Sinclair (1982) para *Clupea harengus* frente a la costa este de Canadá, y posiblemente merezca una mayor atención en relación al potencial pesquero y sus variaciones.

INTRODUCTION

Since the advent of concern about the long-term productivity of the seas in the face of man's predation and perturbations, as reviewed in Thomasson (ed. 1981), there have been numerous general attempts to quantify system potentials, either via attempted simplification utilizing trophic concepts (Hardy 1924, Steele 1974, Cushing 1971), or through study of life table statistics arising from samples taken from fisheries and research ventures on many species (Beverton and Holt, 1957, Ricker 1958, Andersen and Ursin 1977). Numerous techniques have been applied toward obtaining estimates of the amounts, distributions and status of fishery resources. As yet no technique has been particularly successful at projecting fishery production, primarily due to the species and physical oceanographic variations arising from complex climatic and biophysical interactions.

As various management regimes have failed to stabilize fish populations, and therefore production for one reason or another (e.g. Saetersdal 1980), the recent generation of stock assessment specialists is once again opening their ranks and fora to discussions of what variables beyond fishery statistics need to be considered in order to resolve or interpret the variations in population production.

There have been few revolutionary concepts introduced since the early insights of Johan Hjort (1914); Baronov (1918), Michael Graham (1935); or Peterson (1894). The variety of permutations and analytical approaches arising from these original observations, assertions, and interpretations are reasonably well documented in the recent surge of "how to" stock assessment manuals (Laurec and Le Guen 1981, Beyer and Sparre 1983, Pauly, MS). The latter reference even provides examples and programmes on magnetic cards for use with small desk top programmable calculators. These manuals cover virtually all conventional stock assessment techniques. This makes available the possibility to do the rather trivial mathematical operations in single species stock assessment to anyone capable of acquiring data and entering them into a keyboard, and leaves far more time to think about the more difficult problems of interpreting the results, and deciding what new or other parameters need to be incorporated in order to rationalize fishery management.

The more complex models incorporating more than one species are not so readily available. Laevastu and Larkins (1981) have provided an introduction to the ecosystem model which evolved at the Northwest and Alaska Fisheries Center in Seattle, Washington. This model comprises many thousands of computer statements and as such cannot be rightly condensed so as to operate on a desk calculator. Laevastu has however created a "teaching tool" version of the biological interactions segments of the ecosystem model which is available upon request.

Perhaps more important is the general trend in development of the conventional wisdoms to include, once again, ambient environmental (biotic and abiotic) parameters into stock assessment techniques. This has come about through the increasing awareness of the importance of early life history survival requirements, and causes of mortality associated with predation, starvation, and environmental perturbation, i.e. pollution or habitat destruction.

No attempt will be made here to review the so-called stock-recruitement problem, as this has been quite thoroughly done by Ricker (1954); Sharp and others in IOC Workshop Report No. 28 for oviparous fishes; Garcia (in press) for penaeid shrimp; and Hennemuth _et al_., (1981) for a variety of species. The further information needed in relation to the S/R problem is outlined in Bakun _et al_., (1982), and Sharp (1981a) and will be one subject of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Stocks in Costa Rica from 18 to 29 April 1983.

What is becoming increasingly apparent is the relevance of smaller scale ocean processes in setting the limiting survival factors for each component of potential breeders in marine populations. This follows directly from the insights of the early fishery scientists mentioned above, but has grown to be of major research concern only in the recent decades. This is not to say that there has not been substantial continuing effort since G.M. Dannevig released the first few hundred thousand _Gadus_ _morhua_ larvae hatched at the Flødevigen Sea Fish Hatchery in 1886. But even at that time there were heated arguments over what caused the natural variations in cod populations. The eventual instigator of the "critical period" concept, Johan Hjort, was one of the leading critics at the onset of this project. Now, one hundred years later, Norwegian scientists are re-emphasizing the field of enhancement of natural populations through laboratory rearing, sea ranching and release programmes, with scaled feasibility studies as a basis for each stage in development (Sharp 1981c).

The major advocates of increasingly sophisticated studies of larval fish requirements have been Rosenthal (197[illegible]), Jones (1974), Lasker (1975, 1978), Laurence and Beyer (1981), Houde (1974, 1975, 1978 and 1980) and recently IMARPE staff at Callao, Peru. Theilacker and Dorsey (1981) reviewed relevant research results and have made several observations and recommendations regarding required standardization of techniques and reporting of results of studies of larval fish feeding, survival and growth, if such studies are ever to be compared in a meaningful fashion.

Cannibalism and predation on larval and juvenile fishes is recognized as the major mortality source resulting from other than larval fish feeding requirements (MacCall 1981; Smith and Lasker 1978; Andersen and Ursin 1977; Alvariño 1980).

Other parameters which need more attention are those for physical processes which have been identified as important to the early life history stages and adults as well, namely gyres, frontal systems, horizontal microstructure and eddy systems in general (Bakun and Parrish 1981, Parrish et al., 1981, Owen 1981, Grainger 1980; and Illes and Sinclair 1982). These authors have discussed various neritic fish resources in respect to the physical transport phenomena associated with near shore, coastal fish populations.

Reid et al., (1978) and Voronina (1978), have described oceanic zoogeographic provinces in relation to ocean-scale circulation. The reviews of the hydrodynamics of semi-enclosed seas such as the Gulf of Mexico, the Mediterranean Sea and the Baltic (Nihoul, ed. 1982) indicate strong eddy and gyral phenomena dominate these areas, certainly having significant biological consequences.

What is needed is a catalogue, so to speak, of processes, habitat features and their geographic and temporal distributions so that it might be possible to better understand the phenomena which promote or delimit neritic and oceanic fishery resource production potentials in their realistic, dynamic form.

Illes and Sinclair (1982) have stimulated this particular publication by pointing out the dependence of herring (Clupea harengus) populations, i.e., breeding components, upon gyral strengths, distributions, and persistence. What is implied is that the discontinuity of occurrence of a species on the short or long-term, indicates that there are specific, physically mediated requirements which occur within the same pattern of the species distribution. These are often physical processes which promote essential productivity of food, and, in the case of Atlantic herrings, simultaneously maintain larval coherence within the optimal survival conditions. The more mobile juvenile and adult stages are less "controlled" by the local physical processes, but respond in the case of drastic changes.

Similar phenomena and other transport processes are described by Parrish et al., (1981) which they use to explain the reproductive behavior, species success and general zoogeography of the California Current. Sharp (1981b) reviewed numerous interactive phenomena scaled in relation to species mobility, larval requirements, food production and homing versus opportunistic species which can account for the vast behavioral array and species diversity observed in most regions.

The concept of variable carrying capacities for either early life history stages or adults needs careful consideration. The implications for portrayals of species variations, monitoring and forecasting variations, or hindcasting variations in variously behaving species are determined hierarchically by the magnitudes and variations in the important limiting physical processes, and whether these affect primarily early life history stages, or later stages. The near total dependence of early life history stages upon "local" conditions, in contrast to the numerous behavioral options available to more mobile stages, makes this an important consideration.

Now that the importance of early life history effects is better documented and various criteria for survival are being defined, it would be appropriate to step back from the fine scale processes, and look over the global and system scale properties of neritic zones as a first stage in focussing on the system dynamics relevant to fishery resources and their relative fragility.

Upwelling areas have been well documented as the sources of particularly high coastal nutrient and subsequent biological production (recent review in Richards 1981, Cushing 1972, Glantz and Thompson 1981, and Szekielda et al., 1977). Recent efforts to identify other sources of productivity (Gieske et al., 1979, Owen 1981, Pingree et al., 1978 and Gregg 1980) point to the thermocline - picnocline and their vertical counterparts, recognized as fronts of various types as widely occurring features harboring production in various forms and scales, from meters to kilometers in horizontal dimensions and centimeters to meters in vertical dimensions. Mann (1982) reviews production and energy transfer in coastal systems. Fasham (1978) reviewed the relative inadequacies of conventionally obtained plankton data in resolving these relevant scales of occurrence of ocean productivity. It appears that we are entering another age of discovery in this field, particularly as one takes into account the spontaneity of primary production processes and the responses of fish populations. The relative persistence, dynamics and interactions of fish populations and their invertebrate counterparts, are tied in various fashions to the same physical processes as promote, isolate, and disperse the plankton populations supporting the food webs. As the fish resources usually start out in the plankton, graduating in size and relative independence with time, these physical features which promote production and/or aggregation need to be better defined, monitored and evaluated if we are ever to understand the true resource potential, their dynamics and their distributions. Sverdup was saying this 30 years ago (1952, 1955), Chapman 10 years ago (1972) and Bakun, Beyer, Pauly, Pope and Sharp said it again last year (1982) with perhaps a few more direct links between fish, plankton and physical processes from which to begin.

Shepherd, Pope and Cousens (ICES 1982) have summed up rather well the distinctions between various environmental processes which are likely to directly affect fish resources, from 1) direct physiological effects due to temperature, oxygen, salinity, pressure, etc; 2) disease; 3) feeding effects such as food abundance, food quality, time-space variations, localization of concentrations and competition; and 4) predation, the result of one individual being food for another, hence starting the cycle in 3) again. That these authors were also able to convince themselves that there are indeed statistically verifiable links between young fish survival and climate is satisfying, but not news.

In regard to production of food and sustenance of fish populations, one source of primary production and aggregation phenomena which has only recently been given due consideration is the phenomenon of shelf sea fronts (Anon., 1981). In this collection of studies Holligan (1981) characterizes the primary and related secondary production emanating from northwest European continental shelf fronts. He also classifies variously generated fronts, describing shelf-break fronts, coastal fronts, and the relatively important tidal fronts which have been observed in varying detail. Such observations have been made for the Ushant frontal system which extends around the coast of Brittany into the western English Channel (Pingree et al., 1975, 1977, 1979, Grall et al., 1980), the Celtic Sea front between Ireland and Wales (Savidge 1976; Savidge and Foster 1978), fronts in the Irish Sea (Savidge 1976; Foster et al., 1976; Beardall et al., 1978), the Islay front between northern Ireland and Scotland Pingree et al., 1978; Simpson et al., 1979) and the fronts around the Orkney and Shetland Isles (Pingree et al., 1978; Dooley 1978, and southern North Sea (Harding et al., 1978; Pingree et al., 1978).

Allen and Smith (1981) describe wind driven shelf currents off Oregon, northwest Africa and Peru, each being uniquely controlled, some more by wind, others more by longshore currents and topography. The common denominator of these currents and shelf frontal systems is that they both promote eddy formations (Simpson 1981; James 1981), which through initial nutrient injection can set primary production going and zooplankters and fish aggregating into these systems may provide sufficient additional and recycled nutrients to sustain this production over a relatively longer period. The vortices or eddies may provide perfect larval fish development conditions (Illes and Sinclair 1982) and larger eddies, as for example off Southern California (Owen 1980, 1981, 1982) may provide adequate nutritional aggregation for sustaining fish reproduction, coherence of reproduction products through subsequent developmental processes, and even maintain the young fishes within a specific geographic situation which might not sustain some pelagic populations otherwise (Parrish, Nelson and Bakun 1981).

In recognition of the relevance of shelf fronts to fish aggregation and reproduction, particularly tidally generated shelf fronts, the following general description of what they are all about is offered.

SHELF SEA FRONTS

Tidal shelf sea fronts are regions of strong horizontal variation in density, separating vertically stably stratified and well mixed regimes. Vertical density stratification is generated when there is some buoyant input to the sea, such as through surface heating, or runoff of fresh water (the majority of known tidal fronts are associated with the former mechanism). When water is stably stratified, it has a lower potential energy than the same system would have after complete vertical mixing (since its center of gravity is lower). Hence vertical mixing of the water column requires the input of energy. This comes primarily from tidal stirring and from the surface wind stress (on the North West European shelf, the former is more important (Simpson, Allen and Morris, 1978), while in areas such as the Arabian Gulf tides and wind may exert comparable influences (Hunter, 1982).

The balance between the input of buoyancy (and consequent lowering of the potential energy of the water column), and the addition of energy through mixing determines whether stable stratification will occur. If buoyancy input is high we may get stratification, while if mixing is high we may not. In regions where the buoyancy flux and/or the tidal mixing changes markedly in the horizontal, we may find a change from one condition to the other, generally associated with a strong horizontal gradient (a "front").

The energy argument for the occurrence of tidal fronts was originally given by Simpson and Hunter (1974) who concluded that the presence of such fronts should be predictable from the parameter

$$\frac{h}{\bar{u}^3}$$

where h is the water depth,

and u is the tidal stream velocity

(the reciprocal of this parameter is proportional to the tidal dissipation per unit volume of seawater).

Since the tidal velocity occurs as a cubic power law in the above expression, this parameter covers a wide range in the shelf areas of the world - on the North West European shelf it varies over three orders of magnitude (Simpson, Hughes and Morris, 1977), which means that there is ample scope for the formation of tidal fronts in this region.

Shelf seafronts have generally been associated with buoyancy (i.e., less dense water) added at the surface (e.g., by heating, or freshwater inflow). However, vertical stratification can also be caused by the addition of negative buoyance by processes such as surface evaporation. This case is somewhat different from those considered already, in that surface addition of negative buoyancy (dense water) yields an unstable system (denser water overyling light water) which will overturn, generating some mixing as it does so. However, the resultant water, even if vertically mixed, will still be denser than the water in an adjacent region where the evaporation may be less, and this horizontal density gradient can give rise to vertically sheared flows, the denser water passing underneath the adjacent lighter water. This phenomenon is common in tropical seas where evaporation is often a dominant buoyancy flux - dense water is formed in shallow areas where evaporation is highest (both due to the lower relative humidity near the coast, and (in summer) to the higher sea temperatures near the coast) and where a given rate of evaporation yields a greater density change, leading to an "inverted estuarine" circulation (seaward at the bottom, shoreward at the surface). A good example is the Arabian Gulf. It is quite feasible that horizontal fronts could be generated in such areas by lateral variation of tidal and wind mixing processes.

The physical and biological implications of shelf sea fronts were recently reviewed at a conference organized by the Royal Society (Anon., 1981).

THEORY

A simplified derivation of the "h/u^3" law will be given here. More detailed accounts have been given by Simpson and Hunter, 1974; Fearnhead, 1975; Simpson, Allen and Morris, 1978; and Simpson and Bowers, 1981.

Buoyancy may be described as a density anomaly in the sea water, and its "concentration" may be defined quantitatively by

$$-\,g(\rho-\rho_0) \qquad (1)$$

where g is the acceleration due to gravity,

ρ is the sea water density,

and ρ_0 is a constant reference density

(note that $|\rho-\rho_0| >> \rho_0$).

As this factor depends only on density, it is an intrinsic property of the sea water, and as such is conserved in any system when due consideration is made of any sources and sinks of buoyancy. Buoyancy may be modified by the addition or removal of heat or salt, and it may be transported around the sea like any other "contaminant" (i.e., by deterministic flows ("advection") and by turbulence ("diffusion")). For small additions of heat or salt, the buoyancy change will be proportional to the quantities of heat or salt involved (in the case of evaporation, the removal of fresh water may be interpreted as an addition of salt, if desired).

The addition of buoyancy decreases the potential energy of the water column. It can be shown that the rate of decrease in potential energy, if all the buoyancy is concentrated at the surface is given by

$$\frac{Bh}{2} \quad \text{per unit horizontal area of the sea} \qquad (2)$$

where B is the rate of addition of buoyancy per unit horizontal area of the sea,

and h is the depth of the water column.

(We here choose our zero of potential energy as that of the water column after complete mixing to a uniform density distribution. This formulation neglects any work done by atmospheric pressure if the volume of the water column changes during the mixing process. This assumption is reasonable for small density changes, over which it may be assumed that the density varies proportionally with temperature and salinity.)

If no mixing were applied to the water column the potential energy would decrease continually with a larger and larger density anomaly at the surface. However, the presence of mixing increases the potential energy of the water column and may prevent the formation of stratification. Mixing in the sea is accomplished almost exclusively by turbulence, which is generated by the presence of large-scale shearing flows, predominantly associated with tidal and wind-driven currents. Turbulence removes energy from these currents, and most of this energy finally appears as heat. However a small proportion (of order 1 percent) may be made available for removing any stable stratification, thereby increasing the potential energy of the system. The rate of abstraction of energy from a sheared flow is proportional to the shear stress in the fluid, multiplied by the velocity shear. If we consider the whole water column, then turbulent energy is introduced at the boundaries due to slip in layers associated with these boundaries (the "boundary layers") - the upper one due to the surface wind stress, and the lower one due to the tidal current. Each boundary layer introduces turbulent energy equivalent to the boundary stress multiplied by the "slip velocity" across the layer. Boundary stresses in the sea are generally proportional to the square of the slip velocity

$$\tau = \rho C_D \upsilon^2 \tag{3}$$

where τ is the stress,

ρ is the water density,

C_D is a dimensionless drag coefficient,

and υ is the slip velocity.

The rate of generation of turbulent energy is hence related to the cube of the slip velocity

$$\begin{aligned}\text{Rate of generation} &= \tau\upsilon \text{ per unit horizontal area} \\ &= \rho C_D \upsilon^3 \text{ per unit horizontal area}\end{aligned} \tag{4}$$

For tidal currents, "υ" is approximately the tidal stream velocity, while for wind generated turbulence, it is the surface wind drift (roughly 3 percent of the wind speed).

Simpson and Hunter, 1974, assumed that the quantity of energy available for mixing was related to (4) by a constant of proportionality, ξ

$$\text{Rate of supply of energy for mixing} = \xi \rho C_D \upsilon^3 \tag{5}$$

The onset of stratification of a water column should hence be determined by a balance of (2) and (5) - i.e., there is just enough buoyancy input to overcome the possible gain in potential energy due to mixing

$$\frac{Bh}{2} = \xi \rho C_D \upsilon^3$$

or

$$\frac{h}{\upsilon^3} = \frac{2\xi \rho C_D}{B} \tag{6}$$

If, over a given sea area, the right hand side of (6) is constant, then the region where stratification can just occur (i.e. a "front") should be associated with a constant value of "h/υ^3". This has been shown to be the case for tidal fronts on the North West European shelf (Simpson and Hunter, 1974; Simpson, Hughes and Morris, 1977; Simpson, Allen and Morris, 1978; Pingree and Griffiths, 1978), in the Gulf of St. Lawrence (Pingree and Griffiths, 1980), in the Bering Sea (Schumacher, Kinder, Pashinski and Charnell, 1979), in the Bay of Fundy and Gulf of Maine (Garrett, Keeley and Greenberg, 1978), and in the Cook Strait (Bowman, Kibblewhite and Ash, 1980).

As the parameter "h/υ^3" can vary widely, the logarithm of this quantity is generally used to derive a STRATIFICATION PARAMETER, several of which have been defined

(a) $S_s = LOG_{10}(h/u_s^3)$ (7)

where u_s is the surface tidal current amplitude at Springs,

and h and u_s are in SI units.

(Simpson and Hunter, 1974, and other references associated with Simpson)

(b) $S_p = LOG_{10}\ [h/(C_D < |ut|^3 >)]$ (8)

where $< |ut|^3 >$ is the time average of the depth meaned tidal velocity cubed,

and h and ut are in CGS units.

(Pingree and Griffiths, 1978, 1980)

(c) $S_{G1} = LOG_{10}\ [h/(\rho C_D < |ut|^3 >)]$ (9)

where h, ρ and ut are in SI units.

$S_{G2} = LOG_{10}\ (h/\mho^3)$ (10)

where $\mho$ is the depth-meaned velocity amplitude for mean tides,

and h and $\mho$ are in SI units.

((9) and (10) due to Garrett, Keeley and Greenberg, 1978).

(d) $S_H = LOG_{10}(<|ut|^3>/h)$ (11)

where h and ut are SI units.

(Hunter, 1982)

At a given place, these are related approximately by

$$S_s = S_p + 0.57 = SG_1 - 0.42 = SG_2 - 0.45 = -(S_H + 0.82) \quad (12)$$

For the waters of the North West Europen shelf, the position of a front is predictable approximately from

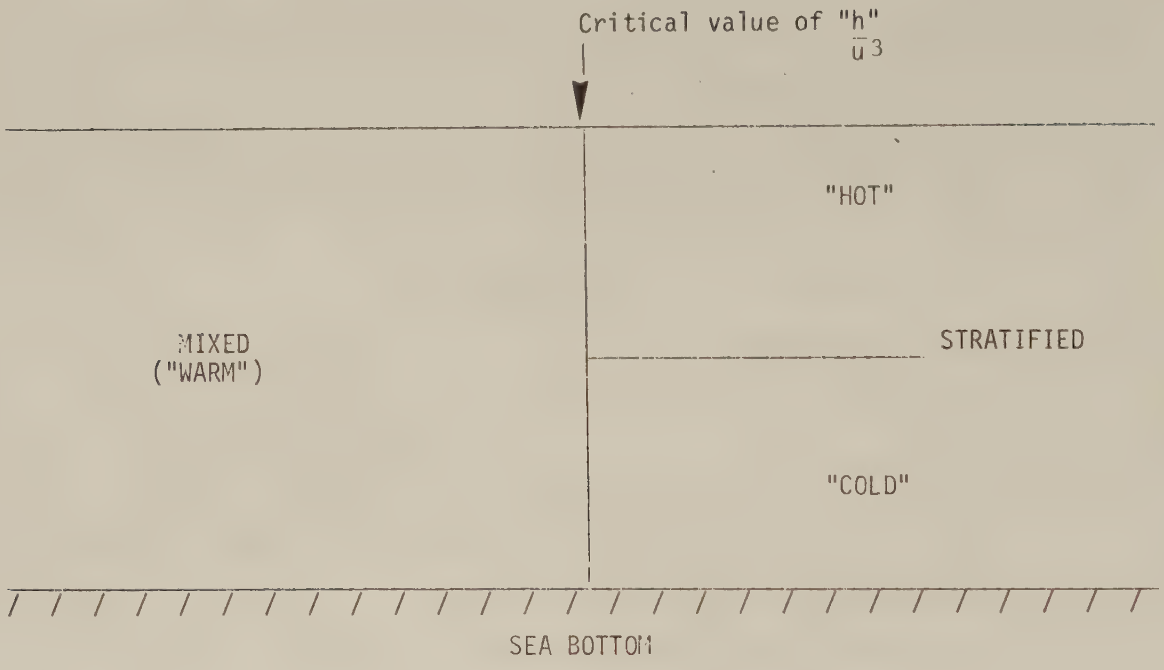
$$S_s = 2 \quad (13)$$

(Simpson, Hughes and Morris, 1977; Pingree and Griffiths, 1978)

In this report the tidal stratification parameter will be loosely referred to as "$LOG_{10}(h/u^3)$" where "u" is one of the definitions of tidal velocity given above.

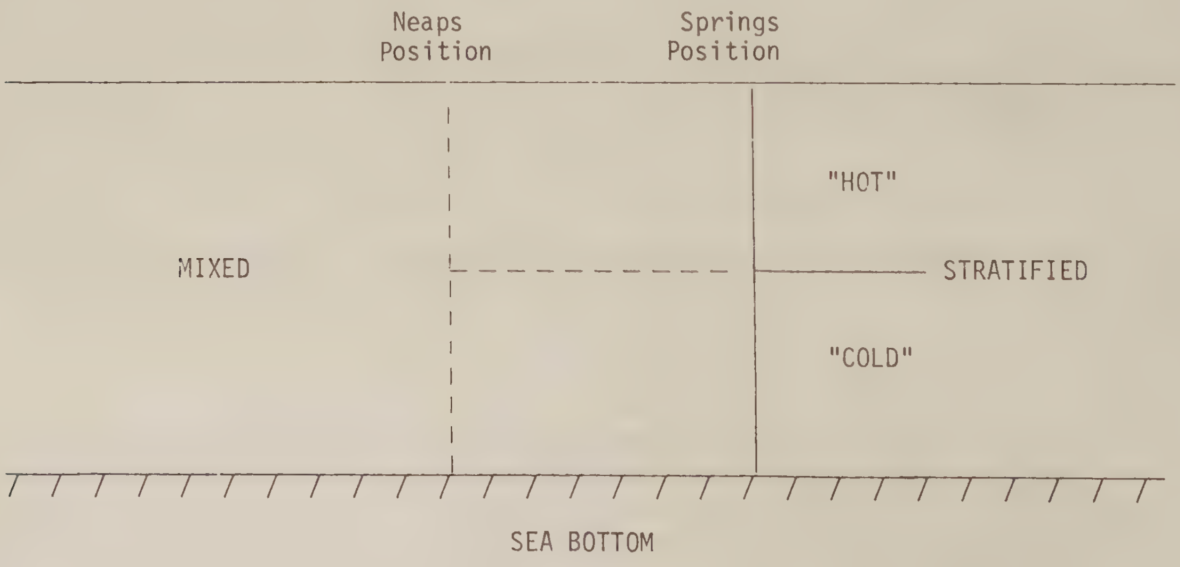
A schematic representation of a front is given below

"$\frac{h}{\bar{u}^3}$" increasing →


Critical value of "$\frac{h}{\bar{u}^3}$"
"HOT"
MIXED
("WARM")
STRATIFIED
"COLD"
SEA BOTTOM

This simple picture of the position of a front fixed in space may be modified by a number of factors

(a) The mixing rate varies over the Springs-Neaps cycle (being a maximum at Springs), so we would expect the position of a front to oscillate over this period, being displaced towards the mixed water at Neaps and towards the stratified water at Springs


Neaps
Position
Springs
Position
"HOT"
MIXED
STRATIFIED
"COLD"
SEA BOTTOM

The expected movement of the front may be calculated from the variation of tidal velocity from Neaps to Springs (and any change in depth associated with the local bathymetry). However, observations have shown that the actual movement that can be attributed to this cause is considerably less than this (Simpson and Bowers, 1979) (the observed Springs/Neaps adjustment is typically 4 km). This discrepancy has apparently been resolved by modifying the simple model, and allowing the efficiency factor for mixing "ξ", to vary with stratification (Simpson and Bowers, 1981) - it is known that vertical stratification inhibits mixing, and so it seems reasonable that "ξ" should decrease with stratification. Simpson and Bowers have shown that such a "variable efficiency" time-dependent model predicts considerably less frontal movement over the Neaps-Springs cycle. This modification to the model also leads to better agreement on frontal position over the summer season - the "constant efficiency" model predicts a marked advance of the front (towards the mixed water) in Spring, and a similar retreat in Autumn, not in accordance with observations, which show an almost constant frontal position from early June to late August (as predicted by the "variable efficiency" model). A further advantage of the variable efficiency model is that it predicts strong horizontal gradients in the degree of vertical stratification (i.e. a sharp front) also in accord with observations.

(b) Frontal positions may also be modified by any water velocity normal to the front. There are several manifestations of this

  (i) Tidal velocities, which advect the front back and forth. This is a major cause of the observed scatter of the positions of a given front in European waters - for a straight front, the displacement is simply given by the component of the tidal excursion normal to the line of the front.

  (ii) Eddy-like features on the front. These have been observed in infra-red satellite images, and may draw their energy from the potential energy of the stratified fluid(baroclinic instability) or from the kinetic energy of the fluid (e.g., from tidal currents). These eddies may have scales of order tens of kilometres, but their dynamics are not well understood.

  (iii) Steady flows. These may systematically distort the line of a front away from the position predicted by "h/u^3" contours, as is probably the case with the front off Islay, to the North of the Irish Sea. In the case of an island, around which a front would be predictable from "h/u^3" values, a wake of mixed water may be formed in the downstream direction (e.g., the Scilly Isles) (see Simpson, 1981, for these examples).

Although the detailed position of a front may be changed from that predictable from a simple "h/u^3" criterion, by the above effects, this basic rule still serves as a good indicator of the areas in which fronts would be expected to occur.

The requirements for the occurrence of a front are mainly twofold

(a) There must be sufficient tidal (or wind) energy to form a mixed region, and conversely there must be adjacent regions where mixing is less and stratification can occur. As a rule of thumb, frontal structures seem to be found in areas of the world known for their high dissipation of tidal energy (e.g. the North West European Shelf, the Bay of Fundy and the Cook Strait).

(b) A condition for the formation of stratification is the supply of buoyancy to the fluid. This buoyancy is equivalent to a certain amount of negative potential energy that must be removed by supplying positive energy if vertical homogeneity is to occur. The relationship between buoyancy and potential energy is however dependent on where the buoyancy is put in - for instance, the potential energy of a column of water may be made more negative by the addition of positive buoyancy (light water) at the surface (the case we have considered up until now) or by the addition of negative buoyancy (heavy water) at the bottom. It is important to understand that the mixing processes described do not remove buoyancy - they simply increase the potential energy in a positive sense. If buoyancy (equivalent, for example, to heat or fresh water) is allowed to accumulate, then eventually some feedback process will "switch off" the buoyancy supply - for the case of heat, the sea will continually warm until surface losses balance the solar heating (as is the case for the daily-averaged conditions of a tropical lake). In such cases, any mixing processes will eventually mix the water vertically, removing any frontal structures originally present. There would appear to be two ways of getting round this problem

(i) If the buoyancy supply is periodic (e.g., seasonal), then during the buoyancy supply phase buoyancy can be stored in the water column, to be removed later during the buoyancy removal phase. This of course is what happens during the summer/winter cycle in non-tropical areas, and is the case for most of the examples of tidal fronts found in the literature.

(ii) The buoyancy may be added at one point in the water column, and removed at another, thereby avoiding any accumulation of buoyancy. For instance, positive buoyancy could be added at the surface and removed at the bottom, thereby decreasing the potential energy of the water column through the formation of a light layer at the surface and a heavy layer at the bottom. This case could be applied to tropical areas and only a simple modification (i.e., a positive and negative buoyancy supply) need be made to the basic model. Frontal positions would still be predictable from "h/u^3" contours, so long as the buoyancy sources were reasonably constant horizontally. The mechanism for the removal of buoyancy from the bottom could be by lateral advection of mixing. A common example of this is an estuary, where positive buoyancy (fresh water) is added at the surface at the landward end and negative buoyancy (salty water) is added at the bottom at the seaward end. On average, no buoyancy accumulates in the estuary, and the negative potential energy input is balanced by tidal and wind mixing. In this example, the flows necessary to maintain the correct buoyancy balance are driven by the horizontal density gradients that arise from the buoyancy inputs - the system adjusts itself to yield a density structure that is roughly constant in time. In regions of an estuary where the mixing levels change in the horizontal, fronts may be formed. The above argument suggests that tropical areas, where the rate of heating does not vary much over the year and where the buoyancy input may be through heating, evaporation or the supply of fresh water, should not be discounted as regions for the possible formation of tidal fronts.

TIDAL MIXING IN SHELF SEAS

For a given rate of buoyancy input, the position of a front should be predictable from a fixed value of "h/u^3". If we consider the value for the North West European shelf, for stratification induced by solar heating, from equation (13)

$$\frac{h}{u_s^3} = 100 \qquad (14)$$

Hence for a typical depth of water over a shelf of 100 metres, the frontal position should coincide with the 1 metre per second surface Spring tidal velocity amplitude contour. As noted in section (2), this represents an area of high tidal dissipation, by global standards.

The tidal dissipation of shelf seas of the world was investigated by Miller (1966). He divided the shelf into 50 regions, and from computations of both the tidal energy crossing the boundaries with the ocean, and of the frictional dissipation at the sea bed, he obtained values of total dissipation for each region. These areas are shown in Figure 1 (from Miller's map), and unfortunately they are of very different sizes, and so do not give a good indication of the energy density available for mixing the water column.

Consider a shelf of length "L" (alongshore), width "W" (offshore) and depth "h". Then from equation (4) the total dissipation of tidal energy over that shelf is given by

$$E = WL\rho C_D <|ut|^3> \qquad (15)$$

where $<|ut|^3>$ is the time average of the tidal velocity

(this may be a depth-meaned value, or a "bottom" value, so long as the drag coefficient "C_D" is chosen appropriately.)

and ρ and C_D are as defined for equation (3).

"E" is the parameter estimated by Miller, and it is related to "$h/<|u|^3>$"

by $$\frac{h}{<|ut|^3>} = \frac{hWL\rho C_D}{E} \qquad (16)$$

Now, "ρ" and "C_D" are approximately constant, and so we need to divide Miller's dissipation values ("E") by the volume of the shelf water ("hWL") to estimate the variation in "h/u^3". This would be a very tedious process, and so a further (rather gross) assumption is made that the depths ("h") and widths ("W") of all shelves are roughly the same. Miller's values have hence been divided by the shelf lengths "L") and used as estimators of the tidal dissipation levels in so far as they effect the "h/u^3" parameter. Hence high levels of "E/L" indicate areas of low "h/u^3", or areas where stratification may be removed by tidal mixing, giving rise to frontal formation.

The computations were performed by measuring shelf lengths on Miller's map (similar to Figure 1), and applying the appropriate scale for that latitude to derive "L". Some modification of Miller's values was made using more recent data (Choi, 1980 (Ryuku Islands); Flather, 1976 (North West European shelf), Sunderman , 1977 (Bering Sea)); and data for the Cook Strait was added (Bowman, Kibblewhite and Ash, 1980). The results are shown in Figure 1, and Table 1. The values of "E/L" have been ranked in descending magnitude (the Okhotsk Sea has the largest value, and is ranked "0"). The numbers shown in the Figure 1, for each region, are the section number (as given in the table), followed by the rank (in brackets).

There are several inconsistencies in Miller's paper, in which cases "best guesses" of the correct values have been made. Some sections of "zero" dissipation were present in Miller's map but not in his table - these have been denoted by "(-)" in Figure 1.

We know that "h/u^3" frontal effects are just apparent in the Gulf of St. Lawrence, a relatively low dissipation area (Pingree and Griffiths, 1980). We may hence regard this as roughly indicative of the lower limit of energy dissipation necessary for the occurrence of frontal structures - hence all regions of rank less than about 23 may exhibit tidal fronts. Examination of Figure 1 indicates the following areas that fulfil this criterion:

(a) The North West European shelf (2), the Gulf of St. Lawrence (22), the Bering Sea (20), the Bay of Fundy and Gulf of Maine (9) and the Cook Strait (4), where tidal fronts have been observed (rank shown in brackets).

(b) Most of the Pacific margin north of the Equator.

(c) The north and east margins of the Indian Ocean.

(d) Australia to the Lesser Sunda Islands.

(e) The south-east and north-east coasts of South America.

(f) The near-Arctic and Arctic areas of the Hudson Strait, the Davis Strait and Norway to Svalbard, all of which must fall into a special category.

It would appear rather ironic that of the shelf regions of the world that have received most attention from oceanographers - the shelves of North West Europe, the U.S.A., Western South America and West Africa, only the former satisfies the above criterion.

An alternative way of looking at the importance of tidal dissipation is to compare the mixing effects of tidal currents and winds. It can be shown (Simpson and Bowers, 1981) that a tidal stream of surface amplitude "u_s" at Springs is equivalent to a root mean cubed wind of

$$9.49\ u_s \qquad (17)$$

Hence for a typical wind of 5 metres per second, a tidal stream of surface Springs amplitude 0.53 metres per second exerts an equivalent mixing effect. Hence for a front to be dominated by tidal effects, we require tidal currents of order 1 metre per second. This also agrees with the criterion derived from actual frontal values of the stratification parameter (equation 14).

THE BUOYANCY SUPPLY TO SHELF SEAS

(a) Surface Heating

The flux of heat through the surface of the sea is by no means determined simply by the rate of solar radiation and the meteorological conditions, since the sea surface temperature plays an important role in the mechanisms involved in dissipating heat (back radiation, and "diffusive" and evaporative heat loss). An isolated lake, continually heated by the sun and atmosphere, will eventually reach an equilibrium temperature at which there is no total heat flux (except for a very small geothermal heat flux upwards). If we know the sea surface temperature, then methods are available for estimating the various flux terms, in order to derive the total heat flux through the surface. An alternative approach is to look at the temperature history of a column of sea water and to thereby derive the total heat supplied to that column over a given period. This latter method takes account of the advection and diffusion of heat into the column from the surrounding sea water, but unfortunately does not tell us where in the water column the heat is introduced (as noted in Section 2, this must be known if we are to be able to compute the rate of input of potential energy to the system) and we are therefore forced to assume that the heat enters at the sea surface.

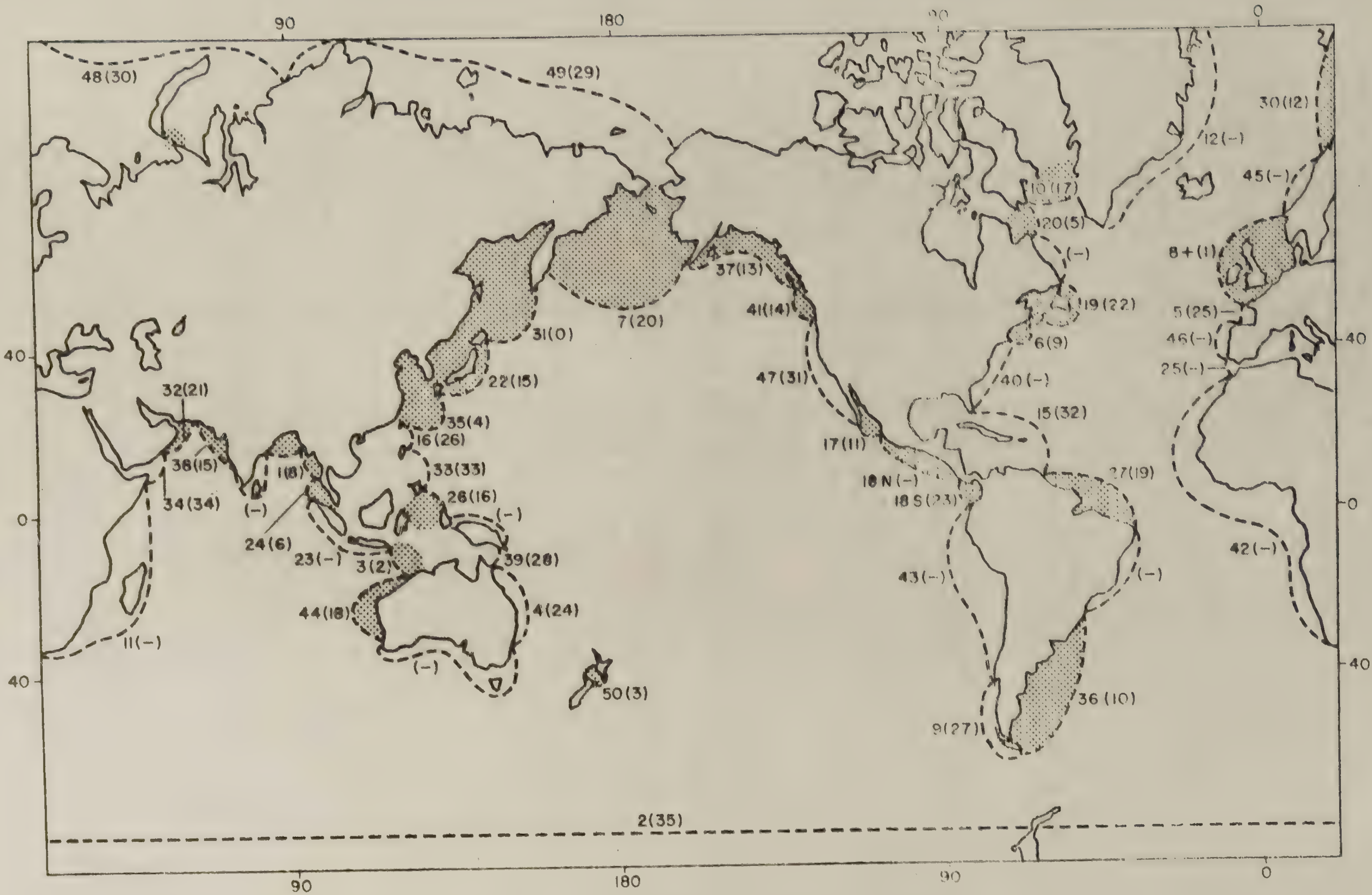
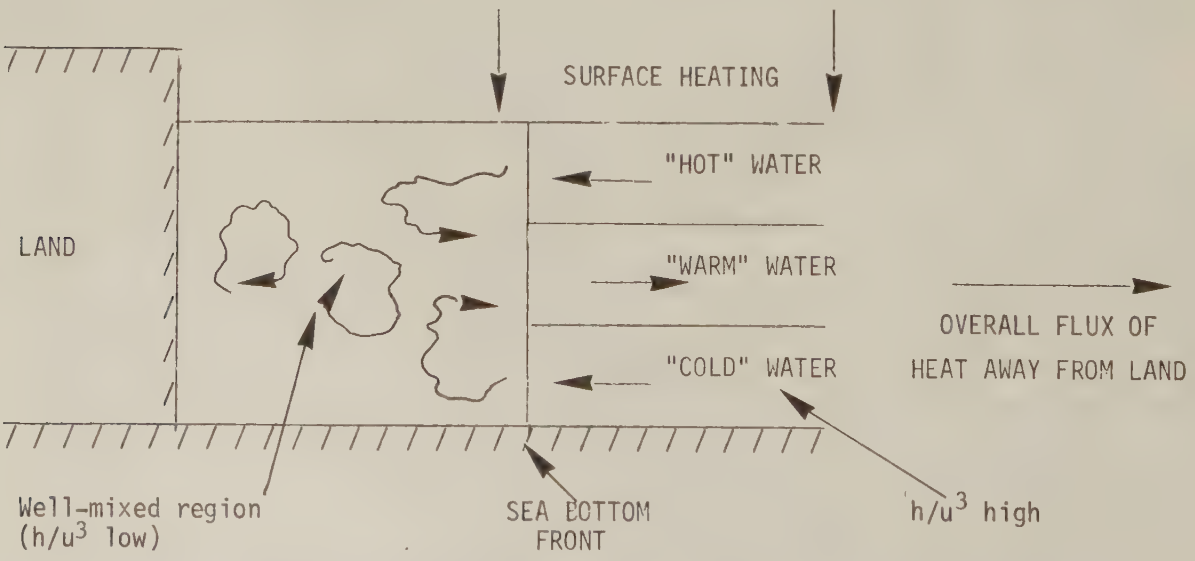

90
180
90
0
48(30)
49(29)
30(12)
12(-)
10(17)
20(5)
45(-)
8+(1)
(-)
37(13)
41(14)
7(20)
31(0)
(-)
19(22)
5(25)
46(-)
6(9)
40
25(-)
40(-)
22(15)
40
32(21)
47(31)
15(32)
35(4)
16(26)
17(11)
38(15)
1(8)
33(33)
27(19)
18N(-)
18S(23)
34(34)
(-)
26(16)
(-)
0
0
24(6)
42(-)
23(-)
3(2)
39(28)
43(-)
(-)
44(18)
4(24)
11(-)
(-)
40
40
50(3)
36(10)
9(27)
2(35)
90
180
90
0

Fig. 1. Tidal dissipation of shelf areas (from Miller, 1966, and others).

Using estimates of the various heat flux terms at the sea surface, Hunter (1982) deduced a total flux of order 100 Joules per square metre per second for the northern part of the Arabian Gulf during the period of maximum heating. From estimates based on the temperature history of a water column on the North West European shelf, Simpson and Bowers, 1981, used a maximum heating rate of 140 Joules per square metre per second in their modelling work. Strokina, 1967, 1969, used this latter approach to produce seasonal maps of the heat flux to the upper layers of the world's oceans. While these are not really appropriate to the shelf areas, due to the strong dependence of the heat flux on sea surface temperature and local meteorology, it is worth noting that for the southern hemisphere the positive heating flux is always less than about 160 Joules per square metre per second. It would hence appear that there is not a wide range in the values of maximum heating flux over the sea. For a factor of 2 change in buoyancy (or heat) flux, the critical stratification parameter (equations (7) to (12) changes by 0.3 For the North West European shelf, the stratification parameter changes by about 1 in 100 kilometres (Pingree and Griffiths, 1978), so a factor of 2 change in buoyancy input would be expected to move the fronts by only about 30 kilometres. Frontal position hence does not depend very strongly on the exact rate of supply of buoyancy.

In non-tropical areas, the heat flux to shelf seas generally shows a well defined annual periodicity. For the North West European shelf, it is positive from mid-March to mid-September (Simpson and Bowers, 1981), and significant stratification exists from April to November (Simpson, Hughes and Morris, 1977). However, the frontal positions are only approximately constant from early June to late August (Simpson, 1981). There would seem to be no reason why these timings should not apply approximately to the rest of the non-tropical northern hemisphere, and, with a shift of 6 months to the non-tropical southern hemisphere.

For tropical areas, where the seasonal change in heating rate over shelf seas is small, it is necessary that there be some mechanisms for the removal of buoyancy if a steady stratification is to develop (as noted in Section 2). A possible system is shown schematically below



The horizontal density gradients induced would drive the circulation necessary to maintain a steady state. For larger systems, Coriolis accelerations would become important and the above two-dimensional circulation pattern would become three-dimensional, with a component of current in a longshore direction.

TABLE 1. TIDAL DISSIPATION OF SHELF AREAS (from Miller, 1966 and others)

Region	No.	Dissipation (ergs/s.x 10^{-17})	Dissipation Per Unit Length (ergs/cm./s. x 10^{-9})	Rank	* = Regions of Potential Tidal Effects
Andaman Sea to 21° N	1	6.5	5.5	8	*
Antarctica	2	0.1	0.006	35	
Australia to Lesser Sunda Islands	3	15	12.4	2	*
Barrier Reef	4	2.4	0.96	24	
Bay of Biscay	5	0.4	0.76	25	
Bay of Fundy and Gulf of Maine	6	2.3	4.9	9	*
Bering Sea	7	2.9	1.4	20	*
N.W. European shelf	8+	21.48	14.2	1	*
Chile	9	0.4	0.28	27	
Davis Strait etc.	10	2	1.9	17	
East Africa	11	0	0	-	
Eastern Greenland	12	0	0	-	
Florida to Trinidad	15	0.3	0.11	32	
Formosa to Luzon	16	0.5	0.65	26	
Gulf of California	17	4	3.2	11	*
Gulf of Panama	18N	0	0	-	
Gulf of Panama	18S	0.6	0.99	23	*
Gulf of St. Lawrence	19	0.8	1.0	22	*
Hudson Strait	20	12	10.7	5	*
Japan Islands	22	4.3	2.3	15	*
Java to Sumatra	23	0	0	-	
Malacca Strait	24	7	7.0	6	*
Mediterranean	25	0	0	-	
Mindanao to N. Guinea	26	2	2.0	16	*
N.E. coast of S. America	27	5	1.6	19	*
North Bay of Bengal	29	6	6.2	7	*
Norway to Svaldbard	30	3.2	3.0	12	*
Okhotsk Sea	31	21	14.6	0	*
Oman-Persian Gulf	32	1.6	1.2	21	*
Philippines	33	0.1	0.083	33	
Red Sea	34	0.2	0.080	34	
Ryukyu Islands	35	11.96	11.3	4	*
S.E. coast of S. America	36	13	3.9	10	*
Southern Alaska	37	5	2.5	13	*
Southern India	38	4	2.3	15	*
Torres Strait	39	0.3	0.25	28	
U.S. east coast	40	0	0	-	
Vancouver, Juan de Fuca	41	1.6	2.4	14	*
West Africa	42	0	0	-	
West S. America, Equator to 42° S	43	0	0	-	
Western Australia	44	4.2	1.8	18	*
Western Norway	45	0	0	-	
Western Spain	46	0	0	-	
Western U.S. to Baja, CA	47	0.4	0.13	31	
Svaldbard to Taimyr	48	0.3	0.16	30	
Taimyr to Pt. Barrow	49	0.6	0.19	29	
Cook Strait	50	2.73	11.4	3	*

(b) Supply or Removal of Fresh Water

In buoyancy terms, the addition of 1 Joule of heat is roughly equivalent to 3×10^{-9} cubic metres of fresh water. Hence a surface heat input of 100 Joules per square metre per second has the same buoyancy effect as the addition of 3×10^{-7} cubic metres per square metre per second of fresh water. This is the equivalent of a river the size of the Mersey, England, discharging 50 cubic metres per second over an area of 170 square kilometres (e.g., a square of side 13 kilometres), or a rainfall equivalent to 3×10^{-7} metres per second or about 10 metres per year (a large figure by global standards). Hence a river may input a significant amount of buoyancy (compared with surface heating) in the region around its mouth (within a few tens of kilometres), but only over short periods could rainfall over the sea input a comparable amount of buoyancy.

During evaporation of water from the sea surface (which is especially important in tropical areas), latent heat is absorbed at a rate of about 2×10^{9} Joules per cubic metre of water. This cubic metre of water is equivalent to about 3×10^{8} Joules of heat supply in buoyancy terms. Hence, from the point of view of the buoyancy supply, the effect of evaporation is mainly to absorb latent heat, thereby cooling the water and adding negative buoyancy (at a rate of 2×10^{9} Joules per cubic metre). The loss of fresh water is only equivalent to about 15 percent of this buoyancy flux (the equivalent of 3×10^{8} Joules per cubic metre).

Over most of the world's oceans, the evaporation rate roughly cancels the precipitation rate (of order 1 metre per year) (Budyko, 1974), so the previous comments concerning the general insignificance of rainfall apply also to evaporation. However, in tropical areas, evaporation may exceed precipitation and become a significant source of negative buoyancy - for example, the average evaporation rate over the Arabian Gulf is of order 1.4 metres per year (Privett, 1959), compared with a rate of precipitation of .14 metres per year (Hydrographer of the Navy, 1967), the difference being equivalent in buoyancy terms to a heat loss of about 13 Joules per square metre per second. Even though this evaporation rate is not particularly high, it is more likely than rainfall to produce local areas of mixed and stratified waters for two reasons:

(i) Rainfall is independent of sea surface temperature and so does not have well-defined localized distributions over the sea. Evaporation, on the other hand is often high in shallow coastal regions due to lower relative humidity and (in the summer) to higher sea surface temperatures near the coast.

(ii) As noted previously, associated with evaporation is an absorption of latent heat equivalent, in buoyancy terms, to about 7 times the fresh water loss.

The dominant buoyancy sources for shelf seas are hence surface heating, river runoff and evaporation. It has been shown above that there are circumstances by which any of these can provide sufficient buoyancy for the formation of frontal structures.

CONCLUSIONS

Tidal shelf sea fronts are associated with regions of relatively high dissipation, areas which are indicated by rank in Figure 1.

Stratification may be induced by surface heating, river runoff or evaporation, and the majority of known tidal frontal structures are associated with seasonal changes of surface heating in non-tropical areas. However, we should not discount tropical areas as to possible sites for tidal fronts, generated by any of the three buoyancy sources, since in the estuaries of the world we have good examples of quasi-steady density stratification being maintained by the interaction of positive buoyancy (fresh water) and negative buoyancy ("ocean" water) under the control of tidal and wind-driven mixing.

For buoyancy input by seasonal heating in the non-tropical northern hemisphere, stratification probably exists from April to November, with stable frontal positions from early June to late August. In the southern hemisphere one would expect these times to be shifted by 6 months.

The characteristic dimensions of fronts and eddies are quite diverse, ranging from short scales of meters to kilometers, corresponding to scales of relevance to larval fish, fish populations, and the aggregation of fishing activities based on "local" resource aggregations. Our knowledge of these events, processes and the dependence of fishery activities related to them needs to be expanded, certainly through more varied scale studies on the processes promoting them in order to better locate them in time and space. It follows that detailed studies of the biological milieu associated with the various features will yield insights into important processes, particularly related to fish reproduction, productivity and energy transfer, and fishery effectiveness measures.

REFERENCES

Allen, J.S. and R.L. Smith. 1981. On the dynamics of wind-driven shelf currents. Phil.Trans.R.Soc. Lond. A302:617-634.

Alvariño, A. 1980. The relation between the distribution of zooplankton predators and anchovy larvae. CALCOFI Reports XXI. (Also ICES, Early Life History Meeting, Woods Hole, April 1979, poster no. 21).

Andersen, K.P. and E. Ursin. 1977. A multispecies extension of the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddr.Damm.Fisk-og Havunders, N.S. 7:319-435.

Anon. 1981. Circulation and fronts in Continental Shelf seas (conference proceedings). Phil.Trans.R. Soc.Lond. A302:515-689.

Bakun, A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean Sciences in relation to living resources. Can.J.Fish.Aquat.Sci. 39(7):1059-1070.

Bakun, A. and R.H. Parrish. 1981. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes (G.D. Sharp, ed.). IOC Workshop Rep. 28. IOC/UNESCO, Paris.

Baronov, F.I. 1918. On the question of the biological basis of fisheries. Nauch.issledov.iktiol, Inst.Izv.I. (1):81-128, Izv.ryb.i nauch.isseldov. I(1) Moscow.

Beardall, J., G.E. Fogg, P. Foster, I. Miller, C.P. Spencer and D. Voltolina. 1978. Biol.Contemp. 5:163-175.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of the exploited fish populations. Fish.Invest., Lond. Ser.2., 19:533 p.

Beyer, J. and P. Sparre. 1983. Modelling exploited fish stocks. In Application of Ecological Modelling in Environmental Management (S.E. Jorgensen, ed.). Elsevier Scientific Publishing Company, Amsterdam.

Bowman, M.J., A.C. Kibblewhite and D.E. Ash. 1980. M2 tidal effects in Greater Cook Strait, New Zealand, J.Geophys.Res. 85(C5):2728-2742.

Budyko, M.I.and D.H. Miller (eds). 1974. Climate and Life. Academic Press. New York. 508 p.

Chapman, W.M. 1972. The application of oceanography to the development and management of ocean fisheries. pp. 13-21. In Progress in Fishery Science. Fifteenth Anniversary Celebration Symposium (R.W. Moore, ed.). University of Washington Press. Univ. of Washington Publications in Fisheries, New Series, Vol. 5.

Choi, B.H. 1980. A tidal model of the Yellow Sea and the Eastern China Sea, Korean Ocean Research and Development Institute. Report 80-02.

Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J.Cons.int.Explor.Mer. 33:340-362.

____________. 1972. The production cycle and numbers of marine fish. Symp.Zool.Soc., London. 29:213-232.

Dooley, H.D. 1978. The role of axially varying vertical mixing along the path of a current in generating phytoplankton production. Phil.Trans.R.Soc.Lond. A302:649-661.

Fasham, M.J.R. 1978. The statistical and mathematical analysis of plankton patchiness. Oceanogr. Mar.Biol.Ann.Rev. 16:43-79.

Fearnhead, P.G. 1975. On the formation of fronts by tidal mixing around the British Isles, Deep-Sea Res. 22:311-321.

Flather, R.A. 1976. A tidal model of the Northwest European continental shelf. Mem.Soc.R.Sci.Liege, 6e serie, X:141-164.

Foster, P., G. Savidge, G.M. Foster, D.T.E. Hunt and L.B. Pugh. 1976. Multivariate analysis of surface water characteristics in the summer regime of the Western Irish Sea. J.Exp.Mar.Biol.Ecol. 25(2):171-185.

Garcia, S. (in press). The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations. Oceanogr. Trop.

Garrett, C.J.R., J.R. Keeley and D.A. Greenberg. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmosphere-Ocean. 16(4):403-423.

Gieske, W.W.C., G.W. Kraay and M.A. Baars. 1979. Current 14C methods for measuring primary production: gross underestimates in oceanic waters. Netherlands J.of Sea.Res. 13(1):58-78.

Glantz, M.H. and J.D. Thompson (eds.) 1981. Resource Management and Environmental Uncertainty, Lessons from coastal upwelling fisheries. John Wiley and Sons, New York, Chichester, Brisbane, Toronto. 491 p.

Graham, M. 1935. Modern theory of exploiting a fishery, and applications to North Sea trawling. J.Cons.int.Explor.Mer. 10:264-274.

Grainger, R.S.R. 1980. Herring abundance off the west of Ireland in relation to oceanographic variation. J.Cons.int.Explor.Mer. 38(2):180-188.

Grall, J.R., P. Le Corre, J. Le Fevre, Y. Marty and B. Fournier. 1980. Oceans. 6:235-274.

Gregg, M.C. 1980. Microstructure patches in the thermocline. J.Phys.Ocean. 10:915-943.

Harding, D., J.H. Nichols and A.R. Folkard. 1978. Studies on planktonic fish eggs and larvae in relation to environmental conditions in the west central North Sea. Annls.Biol. 33:62-69.

Hardy, A.C. 1924. The herring in relation to its animate environment, Part I. The food and feeding habits of herring. Fish.Invest. Lond., Ser. II, 7, 53 p.

Hennemuth, R.C., J.E. Palmer, B.E. Brown. 1981. A statistical description of recruitment in eighteen selected fish stocks. J.Northw.Atl.Fish.Sci. 1:101-111.

Hjort, J. 1914. Fluctuations in the year classes of important food fishes. 1J.du Conseil. (1):5-38.

Holligan, P.M. 1981. Biological implications of fronts on the Northwest European continental shelf. Phil.Trans.R.Soc, Lond. A302:547-562.

Houde, E.D. 1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar.Biol. 26:271-285.

__________. 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream Archosargus rhomboidalis (L) (Sparidae). J.Fish.Biol. 7:115-127.

__________. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull-Mar.Sci. 28:395-411.

Houde, E.D. and R.C. Schekter. 1981. Functional and developmental responses of fish larvae to varying prey concentrations. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Repp.P.-v.Réun.Cons.int.Explor.Mer. 178.

Hunter, J. 1982. Tidal and stratification/mixing models of Kuwait waters, Kuwait Bulletin of Marine Science (in press).

Hunter, J.R. 1982. The feeding ecology of marine fish larvae. In J.E. Bardach (ed.), The Physiological and Behavioural Manipulation of Food Fish as Production and Management Tools. International Center for Living Aquatic Resources Management, Manila.

Hydrographer of the Navy. 1967. Persian Gulf Pilot. 11th Edition. NP63, London.

Illes, T.D. and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science. 215(4533):627-633.

James, I.D. 1981. Fronts and shelf-circulation models. Phil.Trans.R.Soc. Lond. A302:597-604.

Jones, R. and W.B. Howell. 1974. Some observations on the population dynamics of the larval stage in the common gadoids. pp. 87-102. In The Early Life History of Fish (J.H.S. Blaxter, ed.). Springer-Verlag, New York.

Laevastu, T. and H.A.Larkins. 1981. Marine fisheries ecosystem: its quantitative evaluation and management. Fishing News Books Ltd., Farnham. 159 p.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish.Bull.U.S. 73:453-462.

__________. 1978. Ocean variability and its biological effects-regional review-northeast Pacific. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 173:168-181.

Laurec, A. and J.-C. Le Guen. 1981. Dynamique des Populations Marines Exploites: tome 1, concepts et modeles. Pub. du Centre National pour L'Exploitation des Oceans, CNEXO, Brest. 115 pp.

Laurence, G.C. and J.E. Beyer. 1981. A stochastic dynamic model of growth and mortality in winter flounder larvae (Pseudopleuronectes americanus) reared in the laboratory under experimental conditions. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178.

MacCall, A.D. 1981. The consequence of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as Engraulis. p. 201-217. IOC Workshop Report No. 28. (G.D. Sharp, ed.). IOC/UNESCO, Paris.

Mann, K.H. 1982. Ecology of coastal waters: a systems approach. Studies in Ecology, Volume 8. Blackwell Scientific Publications. Oxford, London, Edinburgh, Boston, Melbourne. 322 pp.

Miller, G.R. 1966. The flux of tidal energy out of the deep oceans. J.Geophys.Res. 71(10):2485-2489.

Nihoul, J.C.J. (ed.). 1982. Hydrodynamics of semi-enclosed seas. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York. 555p.

Owen, R.W. 1980. Eddies of the California current system: physical and ecological characteristics. In the California Islands (D.M. Power, ed.). Santa Barbara Mus.Nat.History (Calif.).

__________. 1981. Patterning of flow and organisms in the larval anchovy environment. pp. 167-200. In IOC Workshop Report No. 28. (G.D. Sharp, ed). UNESCO, Paris.

__________. 1982. Microscale plankton patchiness in the larval anchovy environment. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:364-368.

Parrish, R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol.Oceanogr. 1(2):175-203.

Pauly, D. (Draft). Fish Population Dynamics in Tropical Waters: International Center for Living Aquatic Resources Management, Manila.

Petersen, C.G.J. 1894. On the biology of our flatfishes and on the decrease of our flatfish fisheries. Rep.Dan.biol.Stn. IV. 147 pp.

Pingree, R.D. and D.K. Griffiths. 1977. The bottom mixed layer on the continental shelf. Estuar.Coast.Mar.Sci. 5:399-413.

__________. 1978. Tidal fronts on the shelf seas around the British Isles. J.Geophys.Res. 83(C9):4615-4622.

__________. 1980. A numerical model of the M2 tide in the Gulf of St. Lawrence, Oceanologica Acta. 3(2):221-225.

Pingree, R.D., P.M. Holligan and G.T. Mardell. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European continental shelf. Deep Sea Res. 25:1011-1028.

__________. 1979. Phytoplankton growth and cyclonic eddies. Nature. 278:245-247.

Pingree, R.D., P.R. Pugh, P.M. Holligan and G.R. Forster. 1975. Nature. 258:672-677.

Privett, D.W. 1959. Monthly charts of evaporation from the N. Indian Ocean (including the Red Sea and the Persian Gulf). Quart.J.Roy.Met.Soc.(Lond.). 85:424-428.

Reid, J.L., E. Brinton, A. Fleminger, E.L. Vernick and J.A. McGowan. 1978. Ocean circulation and marine life. pp. 65-130. In Advances in Oceanography. Plenum Press, New York.

Richards, F.A. (ed.) 1981. Coastal Upwelling. American Geophysical Union, Washington, D.C. 529 pp.

Ricker, W.E. 1954. Stock and recruitment. J.Fish.Res.Bd.Canada. 11:559-623.

__________. 1958. Handbook of computations for biological statistics of fish populations. Bull.Fish.Res.Bd.Canada. No. 119.

Rosenthal, H. 1970. Anfutterung und Wachstum der Larven und Jungfische des Hornhechts Belone belone. Helgolaender Wiss.Meeresuntersuch. 21:320-332.

Saetersdal, G. 1980. A review of past management of some pelagic stocks and its effectiveness. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:505-512.

Savidge, G. 1976. A preliminary study of the distribution of chlorophyll A in the vicinity of fronts in the Celtic and Western Irish Seas. Estuar.Coast.Mar.Sci. 4:617-625.

Savidge, G. and P. Foster. 1978. Plankton biology of a front in the Celtic Sea. Nature, London. 271:155-156.

Schumacher, J.D., T.H. Kinder, D.J. Pashinski and R.L. Charnell. 1979. A structural front over the Continental Shelf of the Eastern Bering Sea. J.Phys.Oceanogr. 9:79-87.

Sharp, G.D. 1981a. Report of the Workshop on the Effects of Environmental Variation on Survival of Larval Pelagic Fishes. pp. 1-47. In Intergovernmental Workshop Series, No. 28 (G.D. Sharp, ed.). UNESCO, Paris.

__________. 1981b. Colonization: modes of opportunism in the ocean. pp. 125-148. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. 20 April-5 May 1980. Lima, Peru. (G.D. Sharp, ed.). IOC Workshop Report series No. 28. IOC/UNESCO, Paris.

Sharp, G.D. 1981c. Report of the expert consultation on the research status and potential of cod rearing in the North Atlantic. Organized in collaboration with the Svanøy Foundation, Svanøy, Norway, 2-9 August 1981. 12 pp.

__________ (ed.). 1981d. Intergovernmental Oceanographic Commission Workshop Report No. 28. Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. 20 April-5 May 1980. Lima, Peru. UNESCO, Paris. 323 p.

Shepherd, J.G., J.G. Pope and R.D. Cousens. 1982. Variations in fish stocks and hypotheses concerning their links with climate. Mini Symposium ICES CM 1982/GEN:6. 22 pp. plus tables and figures.

Simpson, J.H. 1981. The shelf-sea fronts: implications of their existence and behaviour. Phil.Trans.R.Soc.Lond. A:302:531-542.

Simpson, J.H. and D. Bowers. 1979. Shelf-sea fronts' adjustments revealed by satellite IR imagery. Nature. 280(5724):648-651.

__________. 1981. Models of stratification and frontal movement in shelf seas. Deep-Sea Res. 28A(7):727-738.

Simpson, J.H. and J.R. Hunter. 1974. Fronts in the Irish Sea. Nature. 250:404-406.

Simpson, J.H., C.M. Allen and N.C.G. Morris. 1978. Fronts on the Continental Shelf. J.Geophys.Res. 83(C9):4607-4614.

Simpson, J.H., D.G. Hughes and N.C.G. Morris. 1977. The relation of seasonal stratification to tidal mixing on the Continental Shelf. A Voyage of Discovery. Pergamon, pp. 327-340 (Ed. M. Angel).

Simpson, J.H., D.J. Edelston, A. Edwards, N.C.G. Morris and P.B. Tett. 1979. The Islay front: physical structure and phytoplankton distribution, estuarine and coastal. Mar.Sci. 9:713-726.

Smith, P.E. and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp.P.-v.Réun.Cons.int. Explor.Mer. 173:77-84.

Steele, J.H. 1974. The structure of marine ecosystems. Blackwell Scientific Publications. Oxford, London, Edinburgh, Melbourne. 128 pp.

Strokina, L.A. 1967. Determination of variation in the heat content of the oceans. Tr.Gl.Geofiz. Observ. 209:58-69.

____________. 1969. Variation in the heat content of the oceans of the Southern Hemisphere. Tr.Gl.Geofiz.Observ. 249:58-64.

Sunderman, J. 1977. The semi-diurnal principal lunar tide M2 in the Bering Sea, Deutsche Hydrograph.Zeitschr.J. 30(3)93-101.

Sverdup, H.O. 1952. Some remarks on the place of hydrography in fisheries research. Rapp.P--v.Réun.Cons.int.Explor.Mer. CXXXI.p.7.

____________. 1955. The place of physical oceanography in oceanographic research. J.Mar.Res. 14(4):287-294.

Szekielda, K.-H., D.J. Suszkowski and P.S. Tabor. 1977. Skylab investigation of the upwelling off the northwest coast of Africa. J.Cons.int.Explor.Mer. 37(3):205-213.

Theilacker, G. and K.T. Dorsey. 1981. Larval fish diversity, a summary of laboratory and field research. p. 105-142. In IOC Workshop Report No. 28 (G.D. Sharp, ed.). IOC/UNESCO, Paris.

Thomasson, E.M. 1981. Study of the Sea: the development of marine research under the auspices of the International Council for the Exploration of the Sea. Fishing News Books Ltd., Farnham. 256 p.

Voronina, N.M. 1978. Variability of ecosystems. pp. 221-244. In Advances in Oceanography (H. Charnok and G. Deacon, eds). Plenum Press, New York.

VARIABILIDAD FISICA Y BIOLOGICA EN LA REGION MERIDIONAL DEL SISTEMA DE CORRIENTES CHILE-PERU

Por

Patricio A. Bernal*, Fernando L. Robles*(1) y Omar Rojas**

* BIOTECMAR
Pontificia Universidad Católica de Chile
Sede Regional Talcahuano
Casilla 127 - Talcahuano, Chile

** Instituto de Fomento Pesquero-Chile
Casilla 1287
Santiago, Chile

(1) Dirección actual:
Comisión Oceanográfica Intergubernamental
Unesco. Place de Fontenoy 75700
Paris, Francia

Summary

In this study time series of physical oceanographic data (salinity, temperature and geostrophic flow) and biological data (zooplankton biomass, eggs and larvae of *Engraulis ringens* and *Sardinops sagax*)were examined for the ten year period of the 1970's for the southern region of the Chile-Peru Current system.

The principal water masses in the region are characterized and the variations in these experienced in response to the dominant oceanographic regions are also described. Special emphasis is given to the classification of the oceanographic conditions during the "El Niño" and "Anti-El Niño" periods, and their genesis is discussed in relation to the interactions of large scale ocean-atmosphere phenomena.

Estimations of seasonal variability and long-term residual biological variables are given, and the seasonal cycles are characterized. The seasonal zooplankton biomass component represents 50% of the total, in contrast with the California Current where this variable is about 18% on average. On the other hand, for the long-term analysis the residual variance of the eggs and larvae of *E. ringens* and *S. sagax* attain 70%. The inter-annual changes of the biological variables form no consistent pattern during sequential cold and warm periods. However, a reverse relation between spawning intensity is observed between *E. ringers* and *S. sagax* during warm periods. The extension of the distribution of *S. sagax* is documented for the period following the collapse of the anchoveta fishery after the "El Niño" of 1972.

INTRODUCCION

La presentación a esta Consulta de Expertos de una revisión sobre la variabilidad oceanográfica del Sistema de Corrientes de Chile-Perú, requiere de una explicación preliminar. En primer lugar, la mayor variabilidad de los stocks de peces pelágicos que habitan los ecosistemas altamente productivos de los márgenes orientales de los océanos, aparte de factores poblacionales intrínsecos, pareciera estar también asociada a la variabilidad oceanográfica de gran escala observada en dichos sistemas. En segundo lugar, existe una abundante evidencia acumulada que demuestra el impacto que tienen cierto tipo de eventos oceanográficos semi-periódicos sobre las poblaciones de peces pelágicos en explotación, por ejemplo las alteraciones sobre el reclutamiento de la anchoveta peruana, *Engraulis ringens*, causadas por el fenómenos de "El Niño". La predicción de estos eventos es un objetivo significativo en sí mismo para el manejo pesquero en la Región.

En tercer lugar, y quizás la razón de mayor importancia en el contexto de esta reunión, es el notable incremento de capacidad predictiva que se adquiere respecto a las variaciones de los stocks de peces pelágicos, al incorporar estimaciones parametrizadas de la variabilidad oceanográfica en modelos pesqueros. Un ejemplo de esto último lo encontramos en el trabajo de Parrish y MacCall (1978), quienes analizaron la información contenida en series históricas de la captura de la caballa de California (*Scomber japonicus*). Estos autores, utilizando una variedad de relaciones stock-recluta tomadas de la literatura, demostraron que estas, en el mejor de los casos, explicaban un 24% de la varianza total de la serie histórica de capturas para el período 1931-1968. En cambio, mediante la incorporación de términos densidad-independientes modulados por variables oceanográficas, Parrish y MacCall mostraron que el nivel de varianza explicada por estos modelos mixtos llegaba al 75% de la varianza total. Las variables oceanográficas incorporadas son del tipo altura del nivel del mar, un índice de surgencias costeras, un índice de la divergencia oceánica de la capa superficial y la temperatura superficial del mar, variables todas ellas indicativas de procesos oceanográficos dominantes en los sistemas de márgen oriental.

En el presente trabajo, se presenta una caracterización física y biológica de la Región Meridional del Sistema de Corrientes de Chile - Perú, se discute la variabilidad física de baja frecuencia en torno a el fenómeno de El Niño, y finalmente se analiza la variabilidad de baja frecuencia de series históricas de biomasa de zooplancton y de huevos y larvas de anchoveta, *E. ringens*, y sardina, *Sardincps sagax*.

Fuentes de Información

La información oceanográfica que se presenta y discute en este trabajo proviene de datos obtenidos en 80 cruceros realizados en la Región durante el período 1931 a 1973. Una listado exhaustivo de las fuentes se encuentra en Robles (1979). Una importante fracción de la información fue recolectada como resultado del esfuerzo institucional desarrollado por el Instituto de Fomento Pesquero de Chile (IFOP) en la década 1964-1973. El banco de datos oceanográfico-pesqueros de IFOP, que incluye hasta 1980, 207 cruceros de investigación, 120 de los cuales de carácter oceanográfico, ha sido descrito por Cañón (1980), quien entrega la localización de las estaciones, estado de procesamiento y disponibilidad de la información.

La información biológica sobre huevos y larvas de peces y biomasa planctónica, proviene en su totalidad de los archivos del laboratorio de Ictioplancton de IFOP, donde se llevó a cabo la separación, identificación taxonómica, clasificación por estadios de desarrollo y cuantificación del material. El procesamiento automático de dicha información para el período 1964-73 y su posterior análisis se realizó en el Departamento Biotecmar de la Pontificia Universidad Católica de Chile, Sede Regional Talcahuano.

La Oceanografía física del Pacífico Sureste Meridional: caracterización y condiciones medias

En el Océano Pacífico al sur del Ecuador y con centro en las latitudes intermedias, se ubica el giro anticiclónico del Pacífico Sureste. El brazo oriental de este giro, frente a las costas de Sudamérica, lo forma el Sistema de Corrientes de Chile - Perú. La circulación oceánica y las masas de aguas presentes en la Región del Pacífico Sureste, están determinadas principalmente por la presencia de las aguas frías y de baja salinidad que fluyen de sur a norte como parte de este Sistema de Corrientes.

TABLA 1.- MASAS DE AGUAS EN EL PACIFICO SUR ORIENTAL MERIDIONAL

(de: Robles, 1979)

A) Area 1 : 75°-90°W; 18°-35°S

Masas de aguas presentes	Sigma-t	Profundidad m.	Temperatura °C	Salinidad ‰	Oxígeno ml/l
Subtropical superficial (AST)	<25.30	<35	>18.5	>34.8	>5.0
Subantártica (ASA)	25.70-25.90	70 - 130	12.5 - 13.5	34.2 - 34.4	4.1 - 5.6
Ecuatorial subsuperficial (AESS)	26.80-26.90	320 - 370	8.5	34.4 - 34.5	0.9 - 2.2
Intermedia antártica (AIA)	27.10-27.20	540 - 640	5.5 - 6.5	34.4 - 34.4	2.4 - 4.1

B) Area 2 : COSTA-75°; 18°-28°S

Subtropical superficial (AST)	<25.30	<12	>18.5	>34.9	>5.0
Subantártica (ASA)	25.90	25 - 40	14.5	34.7 - 34.8	2.5 - 4.5
Arica-Mejillones	26.40	100 - 110	12.5	34.7 - 34.9	0.6 - 1.0
Ecuatorial subsuperficial (AESS)	26.80	330 - 370	9.5 - 10.5	34.6 - 34.8	0.3 - 0.6
Intermedia antártica (AIA)	27.30	710 - 750	5.5	34.5	1.5 - 1.9

C) Area 3 : COSTA-75°W; 28°-39°S

"Fiordos"	24.70-25.60	10 - 17	13.5 - 17.5	33.9 - 34.2	5.3 - 6.0
Subantártica (ASA)	25.70-26.00	20 - 50	11.5 - 13.5	34.1 - 34.2	4.0 - 5.7
Ecuatorial subsuperficial (AESS)	26.80-26.90	300 - 340	8.5	34.5 - 34.6	0.8 - 1.3
Intermedia antártica (AIA)	27.10-27.20	560 - 600	5.5	34.3 - 34.4	3.8 - 4.1

D) Area 4 : COSTA-77°W; 39°-48°S

"Fiordos"	24.60-25.10	0 - 40	11.5 - 13.5	32.7 - 33.4	5.5 - 6.6
O_2 mínimo	26.60-26.70	152 - 210	8.5 - 9.5	34.1 - 34.4	2.0 - 3.0
Ecuatorial subsuperficial (AESS)	26.90-27.00	290 - 390	6.5 - 7.5	34.3 - 34.4	2.5 - 4.3
Intermedia Antártica (1)	27.10	500 - 530	5.5	34.3	5.0 - 5.2

(1) Sin datos en Invierno.

E) Area 5 (1) 76°-90°W; 35°-48°S

Subantártica (ASA)	25.20-25.30	10 - 30	13.5 - 14.5	33.7 - 34.0	5.9 - 6.2
O_2 mínimo	26.70-26.90	220 - 270	6.5 - 8.5	34.1 - 34.4	3.3 - 5.0
Intermedia antártica (AIA)	27.10	450 - 470	5.5	34.3	5.5 - 5.8

(1) Sin datos en Invierno.

Las principales masas de agua identificables en el Sistema Chileno-Peruano, son: las Aguas Superficiales Sub-Tropicales (ASST), las Aguas Sub-Antárticas (ASA), las Aguas Ecuatoriales Sub-Superficiales (AESS) y las Aguas Intermedias Antárticas (AIA).

Las propiedades más relevantes de estas masas de agua se resumen en la Tabla 1. A continuación se ilustran los patrones promedio de distribución de estas masas de agua durante el verano (Figura 1) e invierno (Figura 2). Durante el verano en la región oceánica (más allá de los 150 Kms. de la costa), la presencia de las ASST se observa a ambos lados de una penetración hacia el norte de las aguas subantárticas (ASA) entre los 75° - 85°W. La ASST se caracteriza por un máximo de salinidad superficial con valores de 34.8 a 35.0 o/oo, por lo que su límite se muestra en la Figura 1 demarcado por la isohalina de 35 o/oo. Aguas pertenecientes a la ASST se observan generalmente sólo hasta los 30 m. de profundidad. Un amplio rango de temperaturas entre los 15° y los 24° se asocian al máximo salino. Centrada en los 72° 30' W. las ASST presentan una penetración costera hacia el sur que alcanza latitudes de 25° - 27°S en verano y de 23° - 25°S en invierno.

Las aguas sub-antárticas (ASA) son el elemento regional dominante en las capas superficiales. Estas son aguas frías, entre 10° y 18°C, y de baja salinidad, entre 32.0 o/oo y 34.8 o/oo. La profundidad media del mínimo salino que tipifica a las ASA, decrece desde alrededor de 130 m. en el sector oceánico hasta 40 m. en el sector costero. El derrame hacia el norte de las ASA sigue dos cursos principales, uno oceánico entre 75° y 85°W. y otro más costero a lo largo de los 73° - 74°W.

Las aguas ecuatoriales sub-superficiales (AESS) se identifican por la presencia de un máximo salino sub-superficial con valores de salinidad entre 34.5 o/oo a 34.9 o/oo, asociado a un rango de temperaturas de 7° a 12°C. Las AESS se extienden hacia el sur a lo largo de la costa de Chile hasta cerca de la Isla de Chiloé (42° - 43°S.). La presencia del núcleo del máximo salino sub-superficial característico de esta masa de agua, se mantiene a lo largo de la costa central de Chile alrededor de los 300 m. de profundidad y en general coincide con la capa de mínimo de oxígeno y con la isopicna de 26.8 σ_t, lo que sugiere un desplazamiento de tipo isentrópico. La capa de mínimo de oxígeno cumple un rol importante en el ecosistema de la región, pues las concentraciones de oxígeno que la tipifican entre 1.5 a menos de 0.5 ml O_2/lt, se encuentran entre las más bajas observadas en los océanos, presentándose ocasionalmente en esta capa condiciones de anoxia. Es improbable que la mayoría de las especies marinas, en particular los peces, puedan mantener en forma prolongada sus niveles normales de actividad metabólica al interior de esta capa y para muchas de ellas esta zona está efectivamente excluida de su habitat. Por estas razones se ha sugerido que para algunas especies pelágicas, esta capa podría actuar como refugio ante la presencia de predadores activos (Antezana, 1978).

El agua intermedia antártica (AIA) se identifica por la presencia de un mínimo de salinidad profundo. De sur a norte en la región, los valores de este mínimo se elevan desde 34.2 o/oo a 34.7 o/oo, encontrándose asociados a un estrecho rango de temperaturas entre 4° y 7°C.

Un cuerpo de agua que cumple una importante función en la dinámica del sector costero del centro y norte de Chile y sur del Perú, es el agua de Arica-Mejillones (Robles, 1979). Esta masa de agua se caracteriza por un máximo salino sub-superficial aún más elevado que el de las AESS, con valores entre 34.7 o/oo a 35.0 o/oo y en ocasiones hasta 35.2 o/oo. Asociadas a estas salinidades, se encuentra un rango de temperaturas entre 10° a 15°C. El estrecho derrame costero de estas aguas hacia el sur, es cercanamente isentrópico en la superficie de 26.4 σ_t y se produce a una profundidad media de 100 m. A diferencia del AESS, el agua de Arica-Mejillones alcanza latitudes menores. En verano y en coincidencia con el desarrollo de aguas con altas salinidades tanto superficial como sub-superficialmente en la zona noreste de la región, ellas alcanzan aproximadamente los 34°S. En el invierno se repliegan hasta aproximadamente los 31°S. al parecer en conexión con el avance estacional hacia el norte del agua de baja salinidad de de la corriente de los Fiordos.

Los patrones medios de circulación en la región pueden ser descritos apropiadamente con referencia a la Figura 3, que presenta una sección de velocidad geostróficas relativas a 1000 decibares, calculadas en base a una sección hidrográfica a perpendicular a la costa en los 28° 15' S., efectuada durante le Expedición Scorpio en el otoño de 1967 (SIO-WHOI-MIT, 1969).

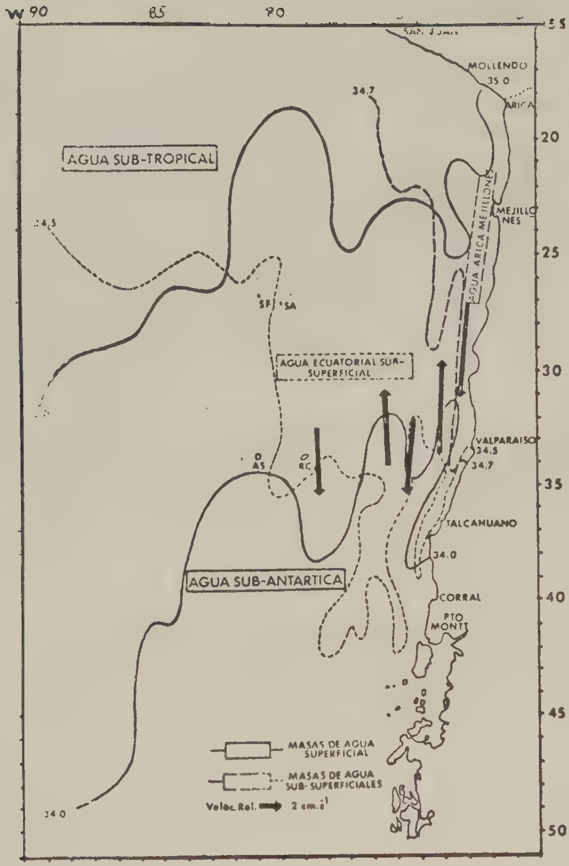
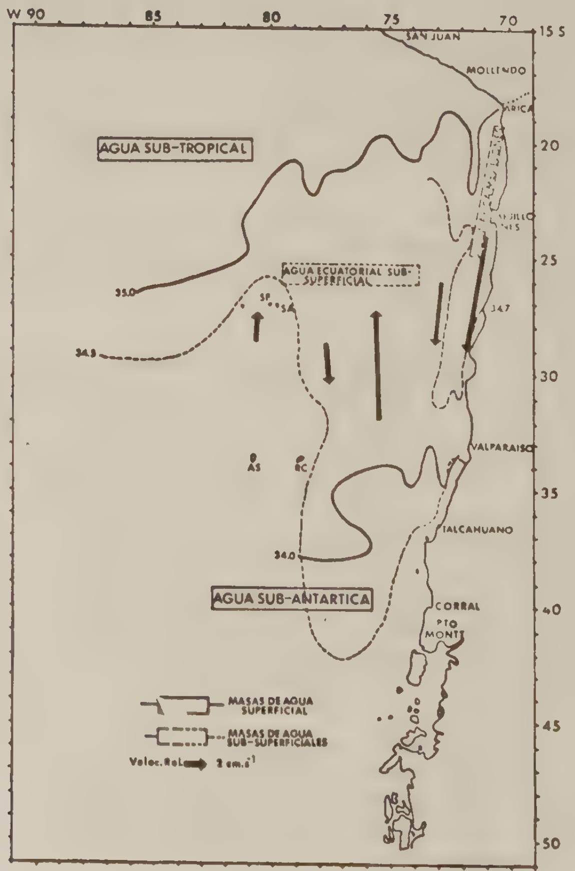

W 90
85
80
15 S
20
25
30
35
40
45
50
MOLLENDO
35.0
ARICA
34.7
AGUA SUB-TROPICAL
MEJILLONES
AGUA ARICA MEJILLONES
34.5
SF
SA
AGUA ECUATORIAL SUB-SUPERFICIAL
VALPARAISO
34.5
34.7
AS
RC
TALCAHUANO
34.0
AGUA SUB-ANTARTICA
CORRAL
PTO MONTT
MASAS DE AGUA SUPERFICIAL
MASAS DE AGUA SUB-SUPERFICIALES
Veloc. Rel. 2 cm.s⁻¹
34.0

Fig. 1.- Masas de agua y circulación en el Pacífico Sureste Meridional durante Verano. Se representa esquemáticamente la extensión de las principales masas de agua superficiales (línea continua) y subsuperficiales (línea de trazos). Los flujos principales del Sistema de Corrientes de Chile-Perú están representados por vectores que indican la dirección del flujo y cuya longitud es proporcional a la velocidad promedio (modificado de Robles, 1979).

Fig. 2.- Masas de agua y circulación en el Pacífico Sureste Meridional durante el invierno. Se representa esquemáticamente la extensión de las principales masas de agua superficial (línea continua) y subsuperficial (línea de trazos). Los flujos principales del Sistema de Corrientes de Chile-Perú están representados por vectores que indican la dirección del flujo y cuya longitud es proporcional a la velocidad promedio (modificado de Robles, 1979).


W 90
85
80
75
70
15 S
20
25
30
35
40
45
50
SAN JUAN
MOLLENDO
ARICA
AGUA SUB-TROPICAL
MEJILLONES
AGUA ECUATORIAL SUB-SUPERFICIAL
35.0
SF
SA
34.5
34.7
VALPARAISO
AS
RC
TALCAHUANO
34.0
AGUA SUB-ANTARTICA
CORRAL
PTO MONTT
MASAS DE AGUA SUPERFICIAL
MASAS DE AGUA SUB-SUPERFICIALES
Veloc. Rel. 2 cm.s⁻¹

El sector oceánico oeste de la zona se ve dominado por un amplio y lento movimiento hacia el norte, con máximos en sus velocidades relativas de alrededor de 4 cm seg^{-1}, ubicados a 1000 o más km de la costa. Este flujo corresponde a la penetración subantártica oceánica, coincidente con el borde oriental del giro anticiclónico del Pacífico Sureste y ha sido denominada la Corriente Oceánica Chileno-Peruana (Robles, Alarcón y Ulloa 1980).

Hacia la costa, se observa un flujo hacia el sur, que de acuerdo a Wyrtki (1967), entra en la región alrededor de los 79ºW, para seguir luego un curso paralelo a la costa a lo largo de los meridianos 76º-77ºW, a 500 km. de la costa. Este flujo ha sido denominado por Wyrtki la Contracorriente Oceánica Peruana, y en la sección de la Figura 3 aparece representado con un máximo de velocidad de alrededor de 6 cm. seg^{-1} a 300 m de profundidad.

Entre 300 y 400 km. de la costa se aprecia el flujo comparativamente más rápido de la Corriente de Humboldt, con un núcleo de máximas velocidades relativas de más de 18 cm. seg^{-1}, alrededor de los 200 m de profundidad.

Entre la corriente de Humboldt y la costa, eventualmente pueden identificarse otros tres flujos, cuya presencia y constancia es más variable, particularmente en relación al dominio de períodos fríos o cálidos en el Pacífico Sureste. El más permanente de estos tres flujos corresponde a una contracorriente , la llamada Contracorriente Costera de Chile (Robles, Alarcón y Ulloa, 1980), que en la Figura 3 aparece desplazándose hacia el sur a aproximadamente 100-200 km de la costa con máximas velocidades relativas en superficie de 10 cm seg^{-1}.

El segundo flujo detectable en la zona costera, es una corriente muy superficial hacia el norte, cuya presencia es más marcada en asociación a los períodos cálidos. Esta corriente, que por corresponder 1967 a un período frío, no aparece en la Figura 3, ha sido denominada por Robles (1979) la Corriente de los Fiordos. Silva y Sievers (1981), la mencionan como la rama costera de la Corriente de Humboldt. Cuando este flujo superficial se encuentra desarrollado, se desplaza a unos 100 km de la costa, exhibiendo velocidades relativas entre 6 y 16 cm seg^{-1}, pudiendo presentar flujos tipo "jets" con velocidades de hasta 40 cm seg^{-1}. Johnson, Fonseca y Sievers (1980) detectaron por medio de mediciones directas (correntometría) en los 33ºS, un flujo costero superficial hacia el norte de unos 30 m de profundidad, que puede corresponder a la Corriente de los Fiordos. Este flujo fue observado como distinto y superpuesto a una contracorriente subsuperficial relativamente acelerada (25 cm seg^{-1}) cuyo núcleo se ubicaba a 100 m de profundidad.

El tercer flujo de la zona costera, es observable inmediatamente fuera de la costa y refleja en las regiones norte y central de Chile, el derrame hacia el sur de las aguas de Arica-Mejillones. Las velocidades geostróficas máximas de esta contracorriente generalmente fluctúan alrededor de los 20 cm seg^{-1}, localizándose a 200 m de profundidad. En conjunto con la Corriente de los Fiordos, esta contracorriente participa y es afectada por los procesos de afloramiento costero, de manera que dependiendo de la latitud, estación del año, y variabilidad interanual, puede exhibir desde velocidades entre 4 - 6 cm seg^{-1} hasta desplazamientos superficiales y subsuperficiales fuertemente acelerados tipo "jet". En la zona norte de Chile, el núcleo de esta corriente yace a unos 100 m de profundidad al igual que en la costa sur del Perú (Brockmann, Fahrbach, Huyer y Smith, 1980), este núcleo coincide o se ubica sobre la capa de mínimo contenido de oxígeno. En términos generales, este flujo hacia el sur es de bastante permanencia y pareciera corresponder más apropiadamente a la Corriente de Gunther o a la "Perú-Chile undercurrent" mencionadas por diversos autores en la literatura.

El Ecosistema pelágico del margen oriental del Pacífico Sur-este

El Pacífico Sureste y en particular el Sistema de Corrientes de Chile-Perú, es uno de los regímenes oceanográficos del mundo que presenta los más altos niveles de producción biológica. Frente a las costas de Perú se han obtenido mediciones de producción primaria de 11.74 g-Cm^2/día (Ryther et al., 1971). En contraste, a estas mismas latitudes, en el ecosistema del giro central del Pacífico es dable esperar valores de sólo 100 a 300 mg-Cm^2/día, dos órdenes de magnitud menores.

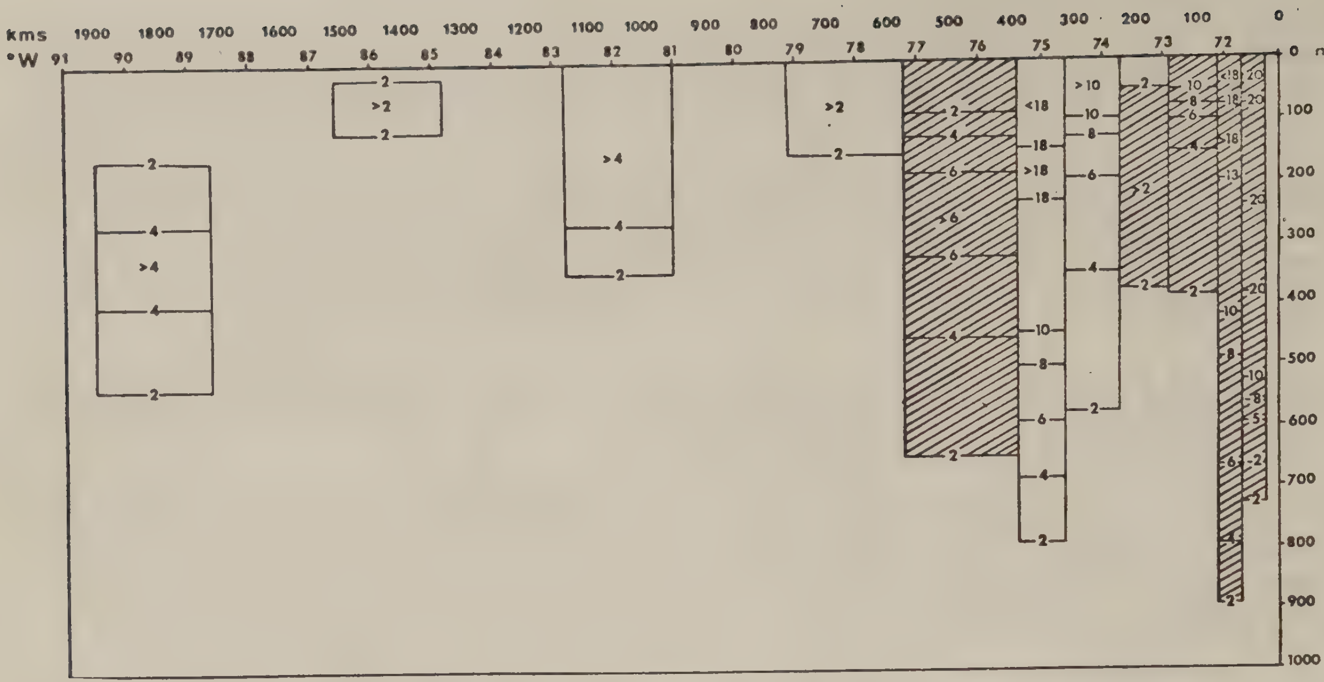


Fig. 3.- Sección de velocidades geostróficas en un corte perpendicular a la Costa en los 28°15'S., Otoño 1967. Las velocidades que se presentan en la figura, están referidas a un nivel de cero movimiento a 1000 decibares y se expresan en cm seg^{-1}. La sección se extiende desde la costa hasta los 91°W (1900 Km de la costa). Los datos utilizados en la confección de esta figura provienen de la Expedición Scorpio (SIO-WHOI-MIT, 1969). Los segmentos achurados indican flujo en dirección al sur y los blancos hacia el norte.

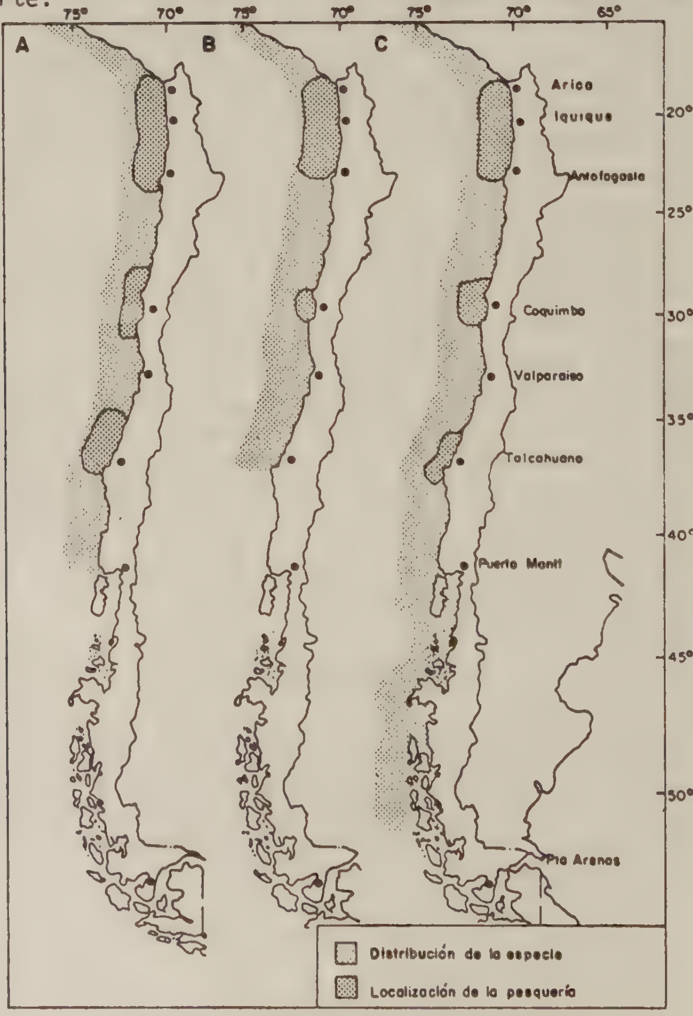

75°
70°
75°
70°
75°
70°
65°
A
B
C
Arica
Iquique
Antofagasta
Coquimbo
Valparaiso
Talcahuano
Puerto Montt
Pta Arenas
20°
25°
30°
35°
40°
45°
50°
Distribución de la especie
Localización de la pesquería

Fig. 4.- Areas de distribución de las principales especies de peces pelágicos y localización de sus pesquerías. A: Anchoveta *Engraulis ringens*; B: Sardina *Sardinops sagax*; C: Jurel *Trachurus murphyi*.

Esta mayor riqueza biológica tiene origen en dos procesos oceanográficos que actúan sinergísticamente. En primer lugar la presencia de surgencias costeras a lo largo del centro y sur del Perú y norte y centro de Chile, que incorporan nutrientes inorgánicos a las capas iluminadas de la superficie; y en segundo lugar el aporte de nutrientes que se incorporan al sistema desde las altas latitudes por advección en los flujos principales del Sistema de Corrientes de Chile-Perú.

Las surgencias costeras tienen lugar en una estrecha banda estrictamente costera, equivalente a un radio de deformación de Rossby. En las latitudes del Pacífico Sureste Meridional, considerando la estratificación observada del campo de densidad en las capas superficiales, esta banda tiene un rango entre 4 a 35 km de ancho. La zona biológicamente enriquecida del Ecosistema por el contrario se extiende mucho más allá de los límites de esta banda, lo que pone de relieve la importancia para el ecosistema de los flujos advectivos de nutrientes.

Por su caracter abierto y con fuerte influencia de la advección, gran parte de la biota presente en el Ecosistema, tiene afinidades con faunas cuyos centros de localización se encuentran fuera del mismo. Además de una fracción menor de componentes endémicos al Pacífico Sureste, en el ecosistema pelágico se encuentran especies de origen subantártico subtropicales, tropicales y cosmopolitas de aguas temperadas. En su borde exterior, aproximadamente a 1000 km de la costa, se ubica la frontera que lo separa del ecosistema del Giro Central del Pacífico Sureste, el que posee una biota propia definida y de mayor diversidad específica.

Los ecosistemas marinos y especialmente aquellos localizados en sistemas de corrientes son estructuras biológicas organizadas cuya fenomenología está dominada en gran medida por procesos físicos, lo que obliga a que cualquier intento de comprender y explicar su dinámica biológica deba considerar esta propiedad. Por estas razones los ecosistemas de margen oriental han sido considerados como ecotonos, ya que los procesos biológicos interactivos clásicos, como competencia y predación, serían secundarios como mecanismos regulatorios al no tener oportunidad de jugar un rol dominante en la modulación de los cambios de abundancia de las especies debido al efecto disruptivo de las cambiantes condiciones físicas (McGowan, 1974).

Los dos procesos físicos responsables de la entrada de nutrientes de origen no-regenerativo al sistema, surgencias y advección horizontal de gran escala presentan una dinámica con una marcada señal estacional. En la región meridional del Pacífico sureste, las surgencias costeras son máximas durante primavera-verano, a diferencia de lo que ocurre en la costa peruana donde son máximas durante invierno. Esta estacionalidad en la costa chilena se origina como respuesta directa al predominio de vientos locales del sur y suroeste, en cambio en Perú debido a la distinta orientación de la línea de costa, se debe al predominio de vientos del sur y sureste.

La estacionalidad en la circulación principal del sistema se acelera e intensifica durante el fin del verano y otoño.

La producción primaria en estas latitudes no es limitada por la disponibilidad de energía radiante, por lo que no es sorprendente que ella siga también un marcado ciclo estacional en respuesta a la disponibilidad de nutrientes inorgánicos en las capas superficiales, principalmente $N\text{-}NO_3$.

Este Ecosistema ha sustentado la pesquería más grande de la historia: la pesquería peruano-chilena de anchoveta en la década del sesenta (objeto de otras contribuciones en este volumen). La Figura 4 muestra las áreas de distribución geográfica y de localización de las pesquerías actuales de la anchoveta, *E. ringens*, sardina española *Sardinops sagax* y Jurel *Trachurus murphyi* en la Región meridional del Pacífico Sureste. En esta región también se explota la caballa *Scomber japonicus*. Esta pesquería, caracterizada por una captura diversificada, contrasta con la pesquería casi monoespecífica sobre *E. ringens* durante la década del sesenta. El ecosistema ha experimentado cambios significativos en cuanto a la composición de su fauna íctica pelágica con posterioridad a el fenómeno de El Niño de 1972, que marcara el colapso de la pesquería de anchoveta peruana.

El más dramático de estos cambios es el aumento de las capturas de *S. sagax* y la extensión hacia el sur de su área de desove, cambio reminiscente del reemplazo inverso de la sardina por la anchoveta en el ecosistema californiano en la década del cincuenta. La captura de *S. sagax* en 1979 alcanzó 1.6 millones de toneladas en Chile y en 1982 llegó cerca de los 2 millones de toneladas.

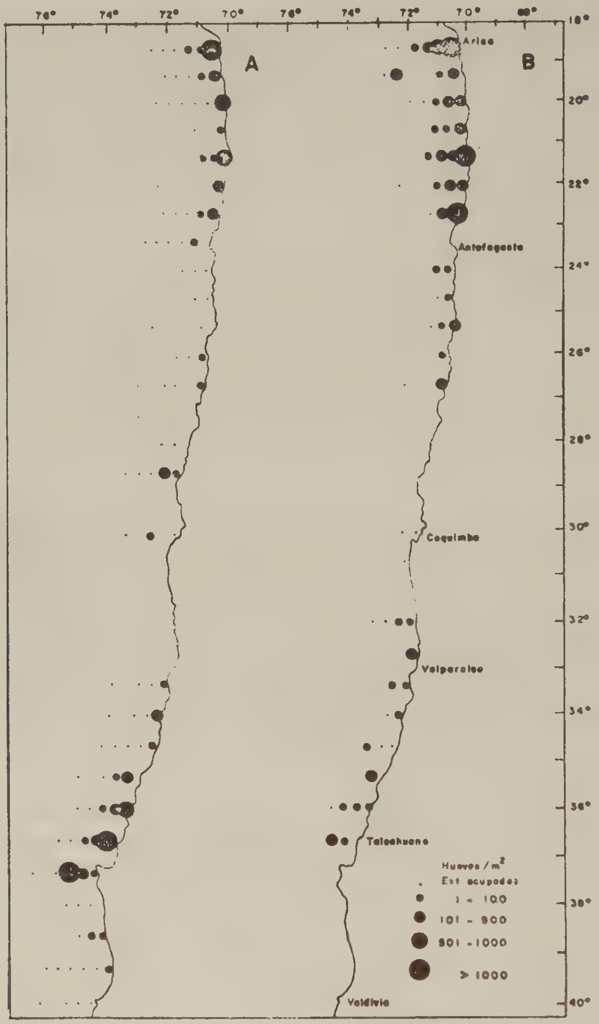


Fig. 5.- Distribución geográfica y abundancia relativa de huevos de anchoveta *Engraulis ringens*, 1963-1973. La abundancia relativa se expresa en huevos/m² de superficie. A: desove de primavera-verano (Noviembre a Enero); B: desove de invierno (Julio a Septiembre). El desove de primavera-verano se encuentra más restringido a la costa, situación que coincide con el predominio de las surgencias costeras en la región.

La Figura 5 presenta la distribución geográfica del desove de *E. ringens* durante el período 1964-1973, basado en datos obtenidos en censos de huevos expresados en huevos/m² de superficie. El desove de primavera-verano (Figura 5a) aparece más restringido a la costa que el desove de invierno (Fig. 5b). Primavera-verano es la época de máxima intensidad de surgencias costeras y en las que éstas se extienden más al sur, lo que coincide con la presencia de un centro de desove en las proximidades de Talcahuano y el Golfo de Arauco (aproximadamente 37°S). En ambos períodos los centros locales de desove con abundancias mayores a 1000 huevos/m², se encuentran inmediatamente adyacentes a la costa y por lo tanto su extensión es conmensurable con el radio de deformación de Rossby. Esto sugiere que la localización de estos centros está conectada a la presencia de centros de surgencia costera.

Variación Oceanográfica de baja frecuencia y el fenómeno de El Niño

Recientemente y como resultado de la disponibilidad de largas series de tiempo en el sistema de la Corriente de California, ha sido posible demostrar que en los sistemas de margen oriental aparte de la clara y estadísticamente definible estacionalidad, existen fluctuaciones de baja frecuencia o de largo período. Esta componente de la variabilidad total de estos sistemas ha sido observada tanto en la dinámica física (Chelton, 1980 y 1981), como en la dinámica biológica (Bernal, 1979 y 1980). Más aún, ha sido posible demostrar que éstas covarían en forma significativa indicando que existe algún grado de acoplamiento entre ambas dinámicas, en el dominio de bajas frecuencias (Bernal, 1981; Chelton y McGowan, 1982).

En el Sistema de Corrientes de Chile-Perú, el fenómeno de El Niño representa la expresión más clara y de mayor importancia de este tipo de variabilidad (Robles, 1979). En términos oceanográficos, El Niño es una invasión masiva de aguas cálidas al sistema de Chile-Perú, alterando la dinámica de sus flujos y la distribución de sus masas de agua. Los eventos de El Niño son la expresión de fenómenos de interacción océano-atmósfera a escala de toda la cuenca del Pacífico mediados a través de mecanismos que se desarrollan a nivel del Pacífico Ecuatorial.

La mecánica de esta interacción se puede conceptualizar en forma simple a partir del balance entre dos tipos de circulación atmosférica: la Circulación de Walker y la Circulación de Hadley. La Circulación de Walker es una celda convectiva de la atmósfera sobre el ecuador que responde a las gradientes térmicas superficiales del océano presentes a lo largo del ecuador. Cuando la temperatura superficial del mar es fría en el Pacífico Este, la convección (i.e. ascensión) de las masas de aire sobre ésta zona se debilita. En estas condiciones el aire desciende hacia la superficie del océano, fluye hacia el oeste para finalmente elevarse sobre las vastas regiones cálidas del Pacífico Oeste (Indonesia, Archipiélago Malayo). La Celda convectiva se cierra mediante el flujo de retorno hacia el este que se efectúa a través de la tropósfera superior. En los niveles bajos de la atmósfera, esta circulación está asociada a presiones atmosféricas altas en el Pacífico Oriental y bajas en el Pacífico Occidental.

La circulación de Hadley es una celda convectiva orientada meridionalmente, producida por la diferencia de temperatura entre el ecuador y las latitudes medias. Cuando en la zona ecuatorial las temperaturas superficiales del mar se presentan anómalamente cálidas, las masas de aire convergen hacia el ecuador, se levantan sobre la zona cálida y fluyen hacia el sureste y noreste por la tropósfera superior. Los vientos Alisios al norte y sur del ecuador se intensifican y por medio de teleconexiones con latitudes medias, aumentan la intensidad de los Vientos Bravos del Oeste, centrados a los 40ºS. Debido a la convergencia, en bajas altitudes la presión atmosférica es anómalamente baja cerca del ecuador y alta en la zona subtropical.

En condiciones normales en el ecuador, el Pacífico Este (adyacente a las costas de Centro y Sudamérica), es comparativamente frío respecto al Pacífico Oeste (Indonesia, Archipiélago Malayo), por lo que la circulación de Walker se presenta bien desarrollada y los vientos de superficie asociados a ella ejercen un esfuerzo (stress) sobre la superficie del mar en dirección al oeste. En condiciones de equilibrio, las capas superficiales del océano responden a esta fuerza de los vientos estableciendo un gradiente de presión de signo contrario, es decir en dirección al este. En una primera aproximación este gradiente puede visualizarse como una mayor elevación de la superficie del mar en las zonas adyacentes a Indonesia.

El Océano y la atmósfera, debido a su distinta capacidad calórica, se calientan (o enfrían) a distintas velocidades. Esta diferencia produce la aparición de extensas zonas de la superficie oceánica con anomalías térmicas positivas y negativas, que actúan como fuentes o captadores del calor atmosférico determinando el predominio de distintos regímenes meteorológicos.

Cuando aparece una anomalía positiva de la temperatura superficial del océano en el Pacífico Este, el gradiente térmico a lo largo del ecuador se debilita, debilitando a su vez la circulación de Walker. El equilibrio entre atmósfera y océano se rompe porque la fuerza (stress) ejercida por el viento no alcanza a balancear el gradiente de presión de las capas superficiales del océano. En las vecindades del Ecuador, donde los efectos de la rotación terrestre sobre las corrientes oceánicas son muy pequeños (el parámetro de Coriolis es idénticamente cero en el Ecuador), este desbalance produce un derrame de aguas cálidas que fluye por la pendiente de presión hacia el Pacífico Este. McCreary (1976) ha modelado este flujo como ondas planetarias de Rossby atrapadas en la singularidad ecuatorial, las que al llegar al continente Americano son atrapadas por el campo de densidad costero en la forma de ondas Kelvin, las que se propagan en forma simétrica hacia ambos hemisferios: norte y sur. Este derrame produce un hundimiento de la picnoclina (o termoclina) y al transportar por advección cantidades importantes de calor causa un aumento adicional de la anomalía térmica inicial. Este mecanismo actúa por lo tanto como un circuito de retroalimentación positiva, ya que provoca una disminución progresiva del gradiente térmico en el Ecuador, lo que torna aún más débil y eventualmente elimina la circulación de Walker.

La suma de estos procesos culmina con el evento de El Niño en el Pacífico Suroriental, donde entre otros efectos se observa el avance hacia el sur a lo largo de la costa norte del Perú, de aguas ecuatoriales superficiales de alta temperatura y baja salinidad, que se extienden considerablemente más al sur de su límite habitual. Otras consecuencias asociadas al fenómeno, son el debilitamiento o cesación del afloramiento costero, lo que permite el acercamiento a la costa de aguas oceánicas de altas temperaturas y altas salinidades. La reaparición de condiciones frías en el Pacífico Este invierte el proceso, reactivando y finalmente manteniendo la circulación de Walker.

Cabe hacer notar que el conocimiento actual sobre el fenómeno de El Niño apunta a su carácter bi-hemisférico. Bernal (1976) presenta evidencias que demuestran la presencia de El Niño de 1957-58 en las costas de California y Chelton, Bernal y McGowan (1982) han demostrado que el aparente nexo entre el flujo de la corriente de California con el forzamiento de los vientos a escala del Pacífico Norte, realmente refleja el acoplamiento de la Corriente de California con la aparición del fenómeno de El Niño en el Pacífico Oriental. Esto último resulta del hecho que a gran escala los vientos sobre el Pacífico norte están significativamente correlacionados con los eventos de El Niño.

Hay una estrecha conexión entre la permanencia de la Circulación de Walker y las variaciones de la llamada "Oscilación del Sur". La Oscilación del Sur implica un intercambio masivo de masas de aire entre el Pacífico Sureste y el Océano Indico Oriental (cerca de Indonesia). La Circulación de Walker es más activa en una situación de la Oscilación del Sur en que el Centro de Altas Presiones del Pacífico Sureste y el Centro de Bajas Presiones de Indonesia se encuentran ambos particularmente desarrollados. La situación inversa, Circulación Walker debilitada, se presenta cuando ambos centros están poco desarrollados. La variación interanual de la Oscilación del Sur se halla también relacionada a anomalías del nivel del mar que se observan a lo largo de una vasta región del margen oriental del Pacífico. De acuerdo a Enfield y Allen (1980), anomalías del nivel del mar registradas entre Crescent City (California) y Antofagasta (Chile), mostraron un alto grado de correlación con las variaciones de la Oscilación del Sur para el mismo período. (P.$<$0.0.1).

Quinn (1974a, b) ha elaborado un Indice de Oscilación del sur en base a las diferencias de presiones atmosféricas entre el centro de Altas Presiones del Pacífico Sureste, tomado en Isla de Pascua, y el Centro de Bajas Presiones de Indonesia, tomado en Darwin, Australia. La Figura 6 muestra para el período 1964-1973 este índice, junto a las desviaciones de temperatura superficial en Chicama, Perú y las desviaciones de la presión atmosférica en Arica, Chile. La concordancia que existe entre estas series de tiempo subraya la gran escala espacial de los procesos envueltos en el fenómeno de El Niño y en los períodos fríos inversos o anti-El Niño. En la Figura 6 se señalan como períodos fríos los años 1964, 1967, 1970-71 y 1973 y como períodos cálidos reconocidos como El Niño, a 1965, 1969 y 1972.

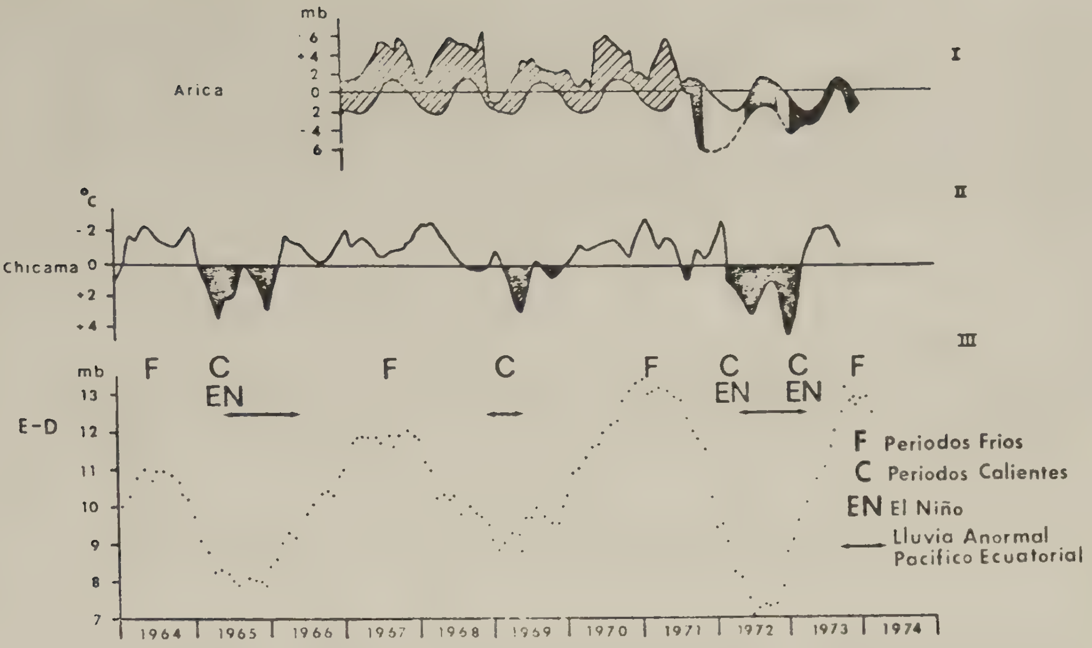


Fig. 6.- Series de tiempo indicativas del fenómeno de El Niño. I. Indice de presión atmosférica en Arica, Chile (de Robles et al., 1976). II. Anomalías de la temperatura superficial del mar en Puerto Chicama, Perú (de Miller y Laurs, 1975). III. Indice de la Oscilación del Sur: presión atmosférica en Isla de Pascua menos la presión atmosférica en Darwin, Australia (de Quinn, 1974a y 1974b). Sobre la serie del Indice de la Oscilación del Sur se indican los períodos fríos (F) y cálidos (C) que se presentaron durante 1964-1974. Las flechas horizontales indican presencia de lluvias anormales en el Pacífico Ecuatorial.

Los períodos fríos (F en la Figura 6) se ven asociados a la intensificación del torque atmosférico y de la circulación oceánica alrededor del centro de Altas Presiones del Pacífico Sureste. En la región meridional del Pacífico Sureste esto se traduce en una intensificación del flujo subantártico hacia el norte, con un dominio en las capas superficiales del océano de bajas temperaturas y bajas salinidades. Inversamente los períodos cálidos (C en la Figura 6) son concurrentes con períodos de relajación en la circulación atmosférica y oceánica del Pacífico Sureste y por lo tanto se suceden a la aparición de grandes diferencias en el Indice de la Oscilación del Sur (E-D en la Figura 6).

De acuerdo a Zuta et al. (1980) las manifestaciones físicas asociadas al fenómeno de El Niño en el Pacífico Suroriental son:

i) un derrame anormal hacia el sur, muy superficial, de aguas de altas temperaturas (23°-29°C) y bajas salinidades (32.5 o/oo - 34.5 o/oo). En la costa peruana estas aguas alcanzan hasta los 14°S;

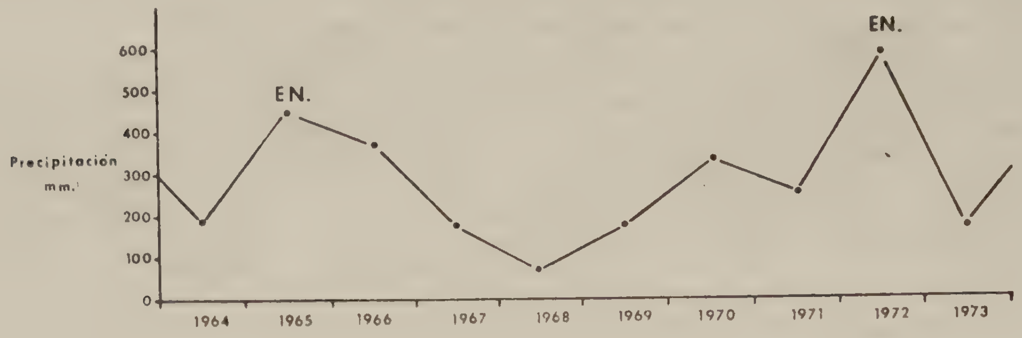
ii) fuertes precipitaciones tropicales que se extienden hasta los 7°S y que superan entre 3 a 10 veces los promedios normales;

iii) un debilitamiento o cese de las surgencias costeras;

iv) aguas oceánicas de altas temperaturas y altas salinidades se aproximan a la costa como producto del debilitamiento de la divergencia costera.

Los dos últimos efectos son característicos a la región Meridional del Pacífico Suroriental.

Una observación importante y que no ha sido suficientemente enfatizada en estudios previos sobre El Niño, precisamente por ser propia a la Región Meridional del Sistema de Chile - Perú, es la drástica disminución de las salinidades en la región costera, en especial en la zona inmediatamente contigua a los fiordos del sur de Chile. Este es un resultado más del calentamiento de gran escala y de la relajación del torque atmosférico y deriva en forma directa del incremento de la pluviosidad en latitudes intermedias y de los aportes de los ríos en las regiones Central y Sur de Chile. Enfield (1981), citando a Miller y Laurs (1975), sugiere que los sistemas ciclónicos pudieran haber tenido más frecuentes desplazamientos hacia el norte durante El Niño de 1972. Esta hipótesis es consistente con la evidencia presentada por Enfield (1981) mostrando que tanto el núcleo de altas velocidades de los vientos como el centro del anticiclón del Pacífico Sureste se localizaron más al norte de sus posiciones normales durante El Niño de 1976 - 77.



PRECIPITACION ANUAL mm. EN SANTIAGO 33°S - 71°W PARA EL PERIODO 1964-1973.

Fig. 7.- Precipitación anual en Santiago de Chile para el período 1964-1973. La precipitación se expresa en mm de agua caída. Máximos de pluviosidad anual que exceden los 420 mm han coincidido con el desarrollo de El Niño. Correlaciones similares se observan con datos de otras estaciones meteorológicas ubicadas en latitudes intermedias.

La Figura 7 muestra los promedios de precipitación anual en Santiago de Chile (33°S, 71°W.), para el período 1964-1973. Los promedios más elevados observados durante el período corresponden precisamente con los dos El Niño más importantes de la década. Si consideramos que el Invierno de 1982 ha sido uno de los más lluviosos en Santiago de Chile, habiéndose producido el desborde del Río Mapocho, un evento no observado en los últimos 50 años, no es demasiado arriesgado sugerir que un El Niño pudiera estarse gestando para la Primavera y Verano de 1982-83.(*)

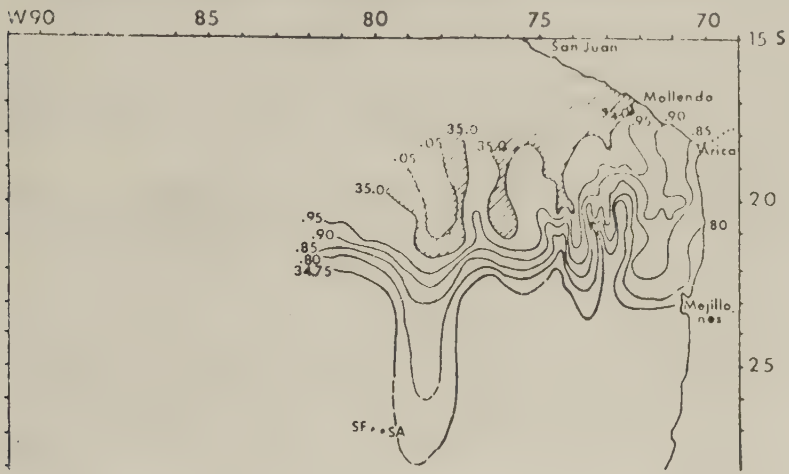
(*) Partes del presente trabajo fueron presentadas al Segundo Seminario-taller Bases Biológicas para el Manejo de Recursos Renovables, realizado en Santiago del 23 al 27 de Agosto de 1982, fecha en la que los datos de precipitación para 1982 no existían. Forrest Miller, de la Comisión Interamericana del Atún Tropical sugirió en Agosto de 1982, en base a los cambios en la estructura térmica y los patrones de circulación de vientos en el Pacífico, el posible desarrollo de El Niño a fines de 1982, información no conocida por los autores a la presentación del trabajo. Entre Agosto de 1982 y la fecha de publicación de este volumen se ha desarrollado un El Niño en la región. En el número 91 del Boletín Informativo de la Comisión Permanente del Pacífico Sur se lee: "El Niño de 1982 se ha presentado a partir de octubre de 1982, con trastornos climáticos y oceanográficos en todo el Pacífico Sureste y, al parecer, asociado a similares trastornos en los más alejados lugares del planeta. Las lluvias muy intensas y persistentes, principalmente en Ecuador, con inundaciones y aluviones están produciendo daños incalculables en vidas humanas, agricultura, viviendas, transporte, subsistencia y salud. Por otro lado, la abrupta disminución de recursos pesqueros, propios de la zona costera, han ocasionado que la industria pesquera en Perú llegue a un estado de emergencia. El Niño de 1982 actualmente en desarrollo, al parecer será el más severo de los últimos 50 años y sólo comparable con aquél de 1925". Aparentemente anomalías positivas en las precipitaciones a latitudes intermedias, son un índice robusto para predecir la presencia de El Niño en Pacífico Sureste Meridional, y puede ser un índice útil a contrastar para la predicción de El Niño de alta intensidad y desarrollo completo en la región de Perú y Ecuador, y el Hemisferio Norte.

Condiciones oceanográficas en el Pacífico Sureste Meridional durante El Niños y Anti-El Niños.

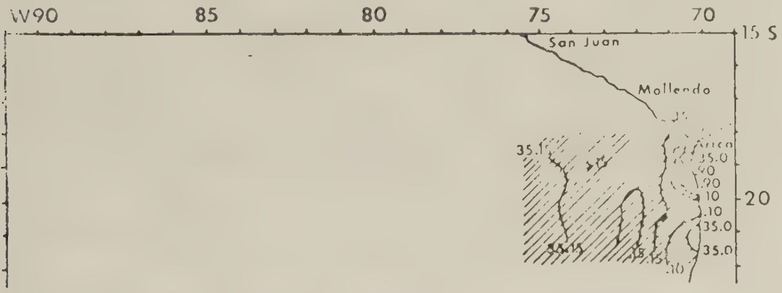
Los cambios en la distribución de las masas de aguas en la zona meridional del Sistema de Corrientes de Chile-Perú durante períodos fríos y cálidos han sido discutidos en detalle por Robles (1979) utilizando el método de los núcleos modales. Esta metodología define los parámetros de una masa de agua que la identifican y permite por lo tanto trazar sus desplazamientos horizontales y verticales en respuesta a cambios en la dinámica del sistema. Estos núcleos corresponden a máximos y mínimos de salinidad que en un diagrama T-S (temperatura-salinidad) se encuentran asociados con un rango constante de temperaturas y por consiguiente con una misma densidad.

A modo de ilustración se han seleccionado tres inviernos, correspondientes a los años 1967, 1972 y 1973. Respectivamente ellos tipifican condiciones durante un año frío, un año de El Niño y condiciones posteriores al evento. En la Figura 8 se muestra la distribución, en la zona entre 17º y 25ºS del máximo de salinidad superficial.

MAXIMO DE SALINIDAD SUPERFICIAL 0/00: Invierno 1967.


W90
85
80
75
70
15 S
20
25
San Juan
Mollendo
Arica
Mejillones
SF
SA
35.0
.05
.95
.90
.85
.80
34.75
80

MAXIMO DE SALINIDAD SUPERFICIAL 0/00: Invierno de 1972.


W90
85
80
75
70
15 S
20
San Juan
Mollendo
Arica
35.1
35.0
.90
.10
35.0

MAXIMO DE SALINIDAD SUPERFICIAL 0/00: Invierno de 1973.

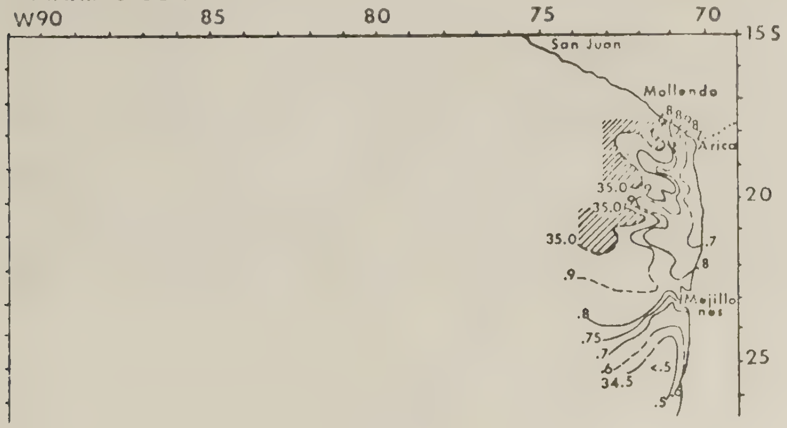

W90
85
80
75
70
15 S
20
25
San Juan
Mollendo
Arica
Mejillones
35.0
.7
.8
.9
.75
.6
34.5
<.5
.5

Fig. 8.- Extensión del máximo de salinidad superficial durante los inviernos de 1967, 1972 y 1973. Areas con salinidades mayores a 35 o/oo se muestran achuradas. El invierno de 1967 es representativo de las condiciones dominantes durante un período frío. En 1972, un año de El Niño, la zona muestreada se encuentra cubierta con aguas de salinidades mayores a 35 o/oo, con excepción de dos pequeños lentes costeros. 1973 presenta condiciones de transición posteriores a El Niño. Ver discusión en el texto.

Durante 1967 las salinidades altas se ven desplazadas hacia el norte en comparación con las condiciones medias. Valores superiores a 35 o/oo, sombreados en la Figura 8, se aprecian hacia el norte de la zona, siendo separados de las regiones costeras por salinidades bajas vinculadas a regiones ubicadas más al Sur. Pueden observarse tres intrusiones de altas salinidades hacia el sur: una a los 78ºW, otra cerca de los 74ºW y la tercera, más disminuída, ocupando la región de Arica-Mejillones. Durante el invierno de 1972, el máximo salino superficial aparece grandemente extendido en comparación con 1967. Las salinidades inferiores a 35.0 o/oo han sido desplazadas hacia el sur y hacia áreas costeras muy restringidas. El patrón predominante es de altas salinidades, homogéneas, que ocupan prácticamente la totalidad del rincón noreste de la región, con solo algunas indicaciones débiles de rasgos observados en 1967, por ejemplo una muy atenuada versión de la lengua de baja salinidad a los 72º-73ºW. En 1973 los núcleos correspondientes al máximo salino superficial, muestran en comparación al invierno de 1972, un retiro generalizado hacia el oeste de las aguas subtropiclaes de alta salinidad. Consecuentemente, las áreas costeras se presentan re-ocupadas por aguas de salinidades relativamente bajas, siendo estos valores aún más bajos que los observados en 1967. Esto puede deberse a que la fuente de las aguas costeras para 1973, debió estar relacionada al mínimo salino costero, el que experimentó un reforzamiento durante el período cálido previo, a causa de la intensificación de la Corriente de los Fiordos. Las bajas salinidades en esta zona serían así aportadas por el re-establecimiento del afloramiento costero que se observó fuertemente debilitado en 1972.

La Figura 9 muestra los cambios en la distribución del núcleo del máximo de salinidad sub-superficial ecuatorial para 1967, 1972 y 1973. Durante 1967 se pueden identificar las siguientes características:

i) en estos niveles la franja costera se observa enteramente ocupada por aguas de altas salinidades con valores mayores de 34.8 o/oo. Estas se extienden hacia el sur desde el rincón noreste de la región, confinadas a un rango de profundidades restringido entre 100 y 150 m;

ii) en la región de Arica-Mejillones, se observa un lente de baja salinidad con valores superiores a 34.75 o/oo ubicado en los 100 m superficiales. Este lente aparece separando la extensión costera hacia el sur de las aguas de alta salinidad en dos ramas: una más litoral cuyo derrame coincide con profundidades entre 100 y 150 m. y otra rama que se proyecta al oeste del lente, a profundidades mayores de 250 m. La rama costera se asocia al agua de Arica-Mejillones. La rama exterior corresponde a la expresión costera del Agua Ecuatorial Sub-Superficial (AESS);

iii) el flujo central de bajas salinidades hacia el norte, limita también en este caso la extensión hacia el oeste de la expresión costera del AESS. El patrón exhibido por el flujo central de bajas salinidades, aparece reducido a una lengua que se extiende a lo largo de los 73º-74ºW. Esta reducción permite un cierto desarrollo hacia el sur de la rama oceánica del AESS, cuyos núcleos alcanzan también profundidades de 250 m;

iv) las salinidades bajas que se observan en la Figura 9 en el sector oeste, corresponden al flujo subantártico oceánico y se ubican en profundidades menores de 200 m.

En 1972 las salinidades se presentan en esta zona, en general, más altas que en 1967, pero en la lente de baja salinidad son correspondientemente más bajas: menos de 34.7 o/oo en 1972 versus más de 34.75 o/oo en 1967. En la zona sur se aprecia la influencia del reforzamiento del sistema de bajas salinidades costeras característico de los años de El Niño, esto se evidencia en la disminución de los valores observados de salinidad en la extensión hacia el sur de la AESS. Esta disminución, comparada con 1967, fue en promedio de 0.2 o/oo. Es interesante recalcar que al margen de la diferencia en los valores de salinidad, el patrón de distribución de la AESS en ambos inviernos es similar. El rasgo más marcado en ambos casos lo constituye la extensión de estas aguas de alta salinidad, a ambos costados de un lente de salinidades relativamente bajas, que permanece en el rincón de la región, frente a la zona de Arica-Mejillones. Al mismo tiempo pareciera que la extensión de la AESS constituye desde la península de Mejillones al sur, una rama costera única.

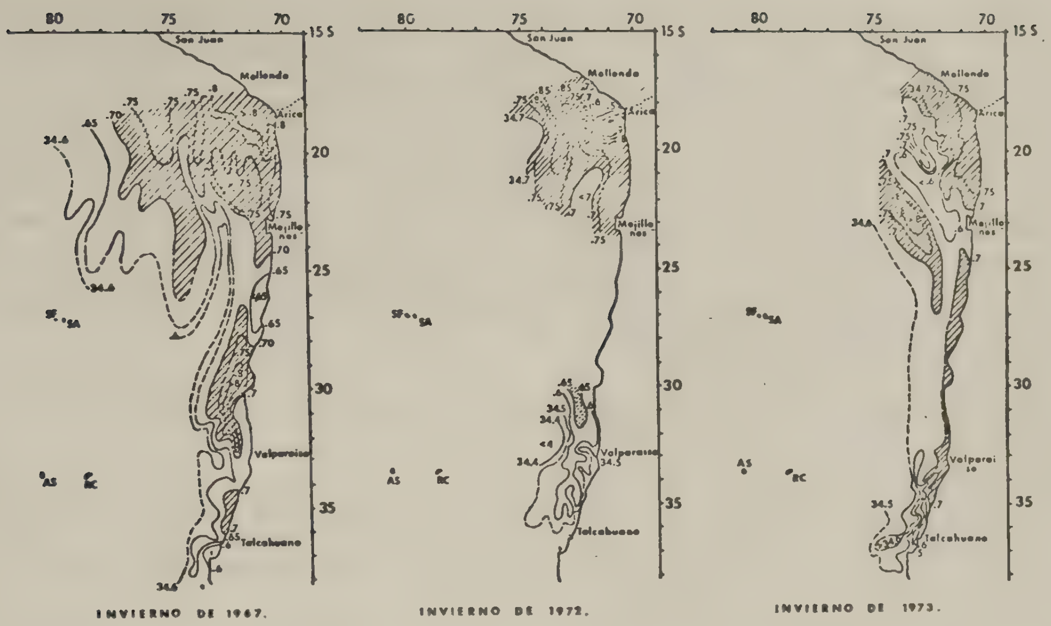

80
75
70
15 S
20
25
30
35
San Juan
Mollendo
Arica
Mejillones
Valparaiso
Talcahuano
SF
SA
AS
BC
34.6
34.7
34.5
34.4
INVIERNO DE 1967.
INVIERNO DE 1972.
INVIERNO DE 1973.

Fig. 9.- Extensión del máximo de salinidad ecuatorial subsuperficial (AESS) durante los inviernos de 1967, 1972 y 1973. Areas con salinidades mayores a 34.70 o/oo se muestran achuradas. Los cambios en la distribución de este núcleo se discuten en el texto.

En 1973 la distribución observada parece representar un patrón de transición entre un período cálido y un período frío. El lente de bajas salinidades, con valores inferiores a 34.6 o/oo, se presenta claramente definido en el rincón noreste de la región. La extensión hacia el sur del núcleo ecuatorial subsuperficial alcanza latitudes mayores que en el invierno de 1972, lo cual es una indicación más del repliegue hacia el sur de la influencia costera de bajas salinidades. Sin embargo salinidades con valores relativamente altos, superiores a 34.8 o/oo, no alcanzan aún las latitudes observadas durante1967.
1967.

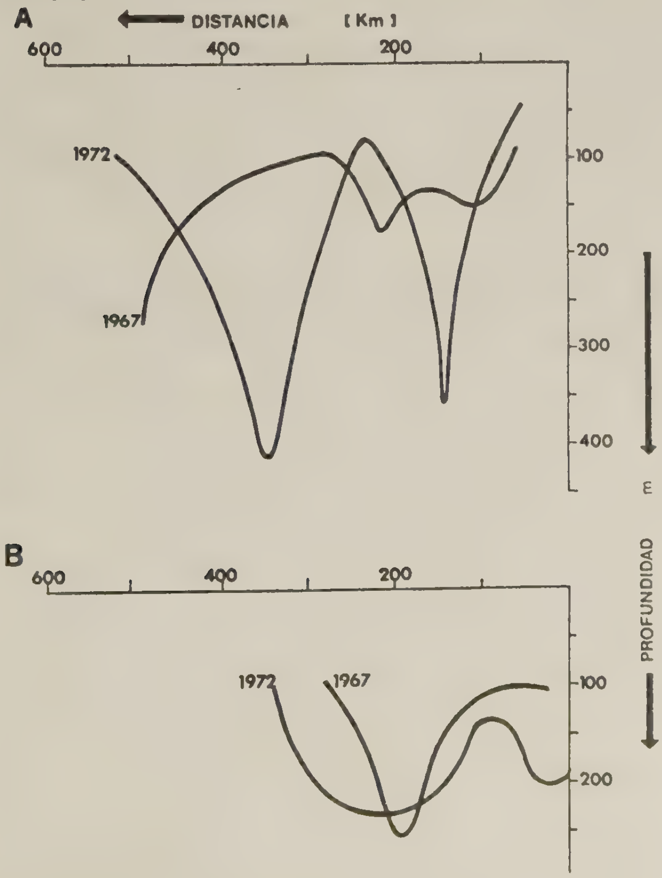


Fig. 10.- Cambios en la topografía del máximo de salinidad ecuatorial Subsuperficial durante El Niño de 1972. A: topografía del Máximo de Salinidad Ecuatorial Sub-superficial en un corte a los 19ºS. durante los inviernos 1967 y 1972. B: topografía del Máximo de Salinidad Ecuatorial Sub-superficial en un corte a los 32ºS durante los inviernos de 1967 y 1972.

Gran parte de los cambios que ocurren en la distribución de las masas de agua en respuesta a la influencia de períodos cálidos y fríos, son reflejados en su distribución vertical. Los núcleos discutidos en las Figuras 8 y 9 experimentan levantamientos y hundimientos considerables en respuesta a la dinámica anómala de estos períodos. La Figura 10 muestra dos ejemplos de los cambios en la topografía del máximo de salinidad ecuatorial sub-superficial en 1967 y 1972. En el panel superior ("A") se muestra la topografía de este núcleo en un corte perpendicular a la costa a los 19ºS, y en el panel inferior ("B") uno a los 32ºS. El contraste entre los períodos fríos y cálidos es más marcado en la zona norte donde se observa un pronunciado hundimiento de este nucleo durante El Niño de 1972. En la zona sur las diferencias de niveles no son tan pronunciadas, excepto en la zona costera, en la que durante 1972 este núcleo se hace más profundo en respuesta a la intensificación del flujo superficial hacia el norte de la aguas menos densas y de bajas salinidades de la Corriente de los Fiordos.

Variabilidad biológica en el sector meridional del Sistema de Corrièntes de Chile-Perú, 1964-1973

La estrecha relación observada en el Sistema de la Corriente de California, entre las variaciones interanuales de la biomasa zooplanctónica y eventos oceanográficos de gran escala asociados a períodos cálidos y fríos en el Pacífico Oriental, (Chelton et al., 1982) permite suponer que una relación similar pudiera ser observable en el Pacífico Sur Oriental.

Como una primera aproximación a esta interrogante, se analizan a continuación series de tiempo (1964-1973) de biomasa del zooplancton, y de huevos de anchoveta, *E. ringens*, y sardina, *S. sagax*, en la región meridional del Sistema de Corrientes de Chile-Perú.

Las muestras de plancton de donde se deriva esta información, provienen de arrastres verticales realizados en los 50 m superficiales con una red Hensen de 0.38 m^2 de boca, equipada con una malla de 300 micras.

El tratamiento de los datos ha sido hecho en forma análoga al tratamiento de la información para la Corriente de California (Bernal, 1980). Los datos de biomasa, expresada como volumen de plancton en ml/1000 m^3 de agua filtrada, han sido convertidos a $\log_e$. Los estimadores mensuales de biomasa y de abundancia de huevos, representan el promedio de todas las observaciones por mes dentro de un área geográfica de acumulación. La Figura 11 muestra las tres áreas de acumulación utilizadas en este estudio. El área I, entre los 18° y 24°S, se caracteriza por presentar una máxima estabilidad vertical a lo largo de todo el año y un mínimo de stress superficial del viento (Bakun y Parrish, 1982). El área II, entre los 24° y 35°S, abarca una zona donde el proceso de surgencia costera es dominante, con claras fluctuaciones estacionales, tanto en la intensidad del stress superficial del viento como en el transporte friccional de Ekman asociado (Bakun y Parrish, 1982). El área III entre los 35º - 40ºS, es una zona dominada por características subantárticas, donde tanto el stress superficial del viento como el transporte de Ekman asociado es muy variable a lo largo del año (Bakun y Parrish, 1982).

El límite oeste de estas áreas de acumulación, se estableció a medio grado de longitud fuera de la costa (56 Km. aproximadamente), límite que dado el carácter restringido de la cobertura horizontal de los datos, incluye cerca del 90% de las observaciones disponibles.

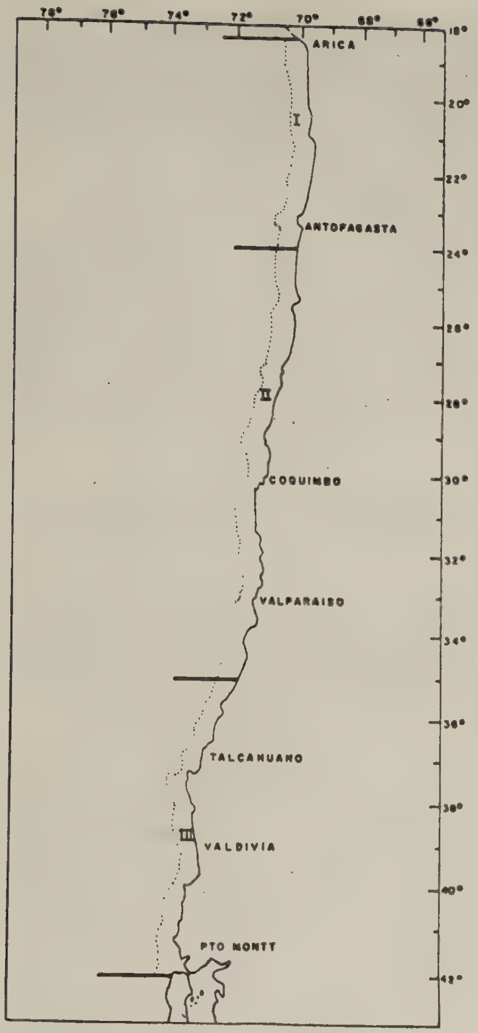

78°
76°
74°
72°
70°
68°
66°
18°
20°
22°
24°
26°
28°
30°
32°
34°
36°
38°
40°
42°
ARICA
I
ANTOFAGASTA
II
COQUIMBO
VALPARAISO
TALCAHUANO
III
VALDIVIA
PTO MONTT

Fig. 11.- Areas geográficas de acumulación. Los estimadores mensuales de biomasa y de abundancia de huevos y larvas de peces representan el promedio de todas las observaciones disponibles para cada área de acumulación. Latitudinalmente las áreas están limitadas por secciones perpendiculares a la costa en los 18°, 24°, 35° y 42° S. El límite mar afuera de cada área está ubicado a 0.5 grados de longitud de la línea de costa (aproximadamente 56 km de ancho), el que se muestra con línea de puntos.

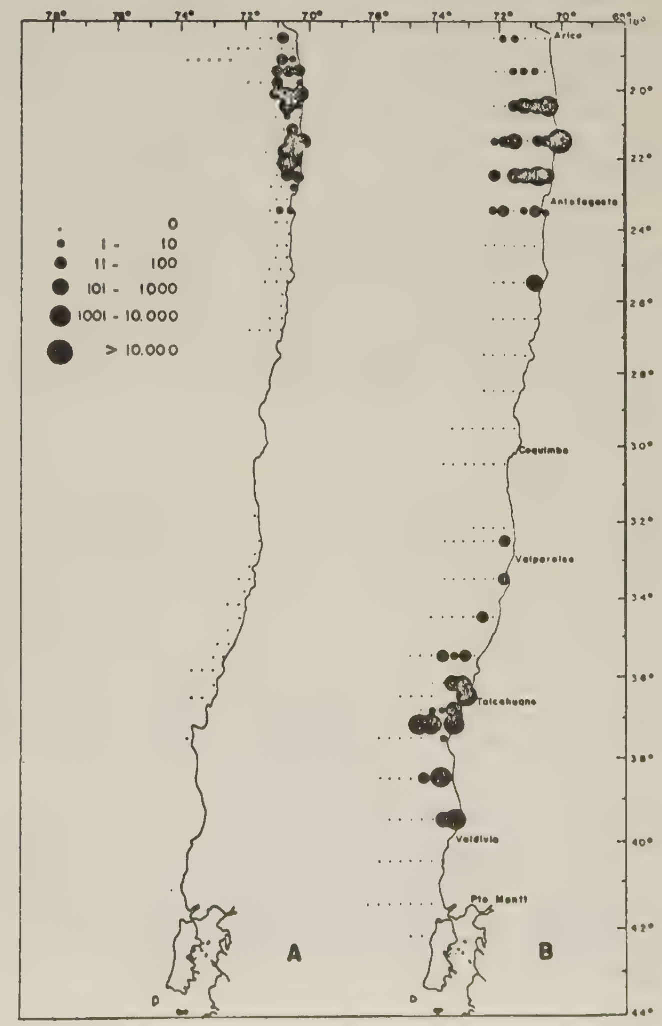

78°
76°
74°
72°
70°
76°
74°
72°
70°
68°
18°
20°
22°
24°
26°
28°
30°
32°
34°
36°
38°
40°
42°
44°
Arica
Antofagasta
Coquimbo
Valparaiso
Talcahuano
Valdivia
Pto Montt
0
1 - 10
11 - 100
101 - 1000
1001 - 10.000
> 10.000
A
B

Fig. 12.- La distribución geográfica y abundancia de huevos de sardina *Sardinops sagax*. A: distribución del desove de sardina para el mes de agosto durante el período 1963-72. El desove se encuentra restringido a la zona entre 18° y 27°S. B: desove de sardina durante agosto de 1981. La distribución del desove de la sardina con posterioridad a El Niño de 1972 muestra un nuevo centro de desove alrededor de Talcahuano y el golfo de Arauco (37°S).

La Tabla 2 resume los valores promedios de las variables para las tres áreas. Los promedios de biomasa fueron calculados sobre todas las observaciones, en cambio para los huevos, se incluyeron sólo los lances de plancton que presentaron huevos en algún estadio de desarrollo. En la Tabla 2, "N" representa el número de meses con estimadores mensuales, y "n" el número total de observaciones incluidas en el promedio respectivo.

TABLA 2.- RESUMEN DE DATOS POR AREAS DE ACUMULACION 1964-1973

	BIOMASA			HUEVOS *E. ringens*			HUEVOS *S. sagax*		
	M.G.	N	n	$\bar{x}$	N	n	$\bar{x}$	N	n
AREA I	372.8	50	(2010)	271.6	54	(735)	42.4	43	(267)
AREA II	256.5	25	(561)	33.9	22	(110)	2.3	4	(7)
AREA III	273.7	15	(170)	350.3	13	(92)	-	-	-

Un primer resultado de este análisis, es la ausencia de un gradiente latitudinal de biomasa. La presencia de un marcado gradiente latitudinal es quizás la característica global más sobresaliente en el Sistema de la Corriente de California, con valores altos en las latitudes mayores. De haberse repetido este patrón en el Pacífico Sur Oriental, se esperarían altos valores en el área III, situación que no se observa.

Los valores de densidad promedio de huevos de anchoveta *E. ringens*, reflejan bastante bien la localización de sus áreas de desove (Figura 5), con máximos en las áreas I y III. Los huevos de sardina, *S. sagax*, son notablemente menos abundantes que los de *E. ringens*, reflejando el dominio de *E. ringens* en el ecosistema durante el período en estudio. En el área II, de 561 muestras analizadas, sólo 7 contenían huevos de *S. sagax* y en el área III de 170 muestras analizadas, nunca se encontró un huevo de *S. sagax* al sur de 35ºS entre 1964-73. Esto contrasta dramáticamente con la situación actual en 1982.

En la Figura 12 se muestra la distribución y abundancia de huevos de *S. sagax* para el período 1964-1973 (Fig. 12A) y para 1981 (Fig. 12B). Se ha escogido el mes de Agosto como representativo de la época de desove. De la comparación de los dos mapas resulta evidente la presencia en 1981 de un nuevo centro de desove alrededor de Talcahuano y el Golfo de Arauco (37ºS), inexistente en la década anterior. Esta colonización hacia el sur de *S. sagax*, es posterior a la declinación del stock de *E. ringens* que siguió a El Niño de 1972 y refleja el reemplazo en el ecosistema del pez epipelágico filtrador dominante.

Santander y Castillo (1977) reportan las variaciones en la intensidad del desove de *S. sagax* en la costa peruana donde se observó una situación similar a la descrita para Chile. Al igual que en Chile, la estacionalidad del desove en Perú presenta también un máximo en Julio-Agosto. Durante el período 1966-1971, para los meses de Julio-Agosto y Septiembre, estos autores informan del análisis de 672 muestras, habiendo encontrado huevos de sardina sólo en 13 de ellas. El cuociente entre el esfuerzo de muestreo y la abundancia total de huevos puede ser considerado como un índice de la disponibilidad de huevos de anchoveta en la costa peruana. Durante este período este índice de disponibilidad fue de 2 huevos/unidad de esfuerzo. Geográficamente este desove se localizó principalmene en las áreas norte y central del Perú, desde Cabo Blanco (4º10'S) hasta Callao (12º05'S).

Durante 1972, Santander y Castillo (1977) observaron la expansión del desove a toda la costa peruana y su concentración por fuera de 35 millas de la costa, aparentemente evitando el área costera de desove de anchoveta. El índice de disponibilidad durante 1972 alcanzó valores de 19 huevos/unidad de esfuerzo. La abundancia promedio de huevos de sardina calculada sobre la base de las muestras positivas en los meses de Julio, Agosto y Septiembre, durante 1966-1971 fue de 103.4 huevos, en cambio durante 1972 fue de 260.2 huevos.

Estos antecedentes sugieren que el área de Arica-Mejillones sirvió durante 1964-1971 como una zona de refugio para las poblaciones de sardina, ya que tanto hacia el norte, en Perú, como hacia el sur, en Chile, el desove de esta especie prácticamente no existió, a excepción de la región entre Cabo Blanco y Salaverry en el norte de Perú donde se observaron esporádicamente centros locales de desove.

Desde el punto de vista de la dinámica y genetica de pobaciones, una hipótesis de trabajo interesante es suponer que durante el predominio de la anchoveta en el ecosistema pelágico de Chile-Perú, las poblaciones de sardina se encontraron restringidas a dos zonas refugio separadas: Cabo Blanco a Salaverry y Arica a Mejillones, habiéndose limitado en forma efectiva el intercambio de información genética entre ambas subpoblaciones. El predominio de la anchoveta fue lo suficientemente largo y las condiciones ambientales lo suficientemente distintas en cada refugio, como para esperar cambios observables con técnicas actuales (p.ej. DNA-mitocondriae) en la variabilidad genética de ambas subpoblaciones, aún después de la expansioón de las poblaciones posterior a El Niño de 1972.

Al respecto es imposible dejar de comparar lo ocurrido en Chile-Perú durante la década del sesenta con lo ocurrido en California en la década del cincuenta. En California durante el predominio de la sardina, *S. caerulea*, las poblaciones de anchoveta, *E. mordax*, se concentraron en la zona de "Los Angeles Bight" (Seno del Sur de California), y en la región de Punta Eugenia en Baja California (Kramer y Ahlstrom, 1968). Con la progresiva expansión de las poblaciones de anchoveta, la sardina ocupó áreas cada vez más restringidas, concentrándose en la zona del Seno del Sur de California (Kramer, 1970), área que ha servido como refugio para la especie.

En un intento de clasificación de los hábitats de las especies de peces pelágicos de las corrientes de Margen Oriental, Bakun y Parrish (1982) presentan climagramas construidos con los valores mensuales del cubo de la velocidad del viento superficial versus la magnitud del transporte de Ekman paralelo y perpendicular a la costa para distintas regiones geográficas de las costas de Norte y Sudamérica. El cubo de la velocidad del viento es una variable indicativa de la tasa de producción de energía de mezcla turbulenta por el viento en las capas superficiales del océano. En esta clasificación, las regiones del Seno del Sur de California en Norteamérica y la zona de Arica, en la frontera chileno-peruana son las que más se asemejan entre sí, presentando a lo largo de todo el año valores muy bajos de las variables de clasificación. Esto indica que estas zonas son particularmente estables desde un punto de vista oceanográfico, estabilidad que al parecer está ligada a una mejor calidad de hábitat para las poblaciones de sardina y anchoveta, quienes las utilizan como refugio durante las épocas de predominio y expansión geográfica de su competidor.

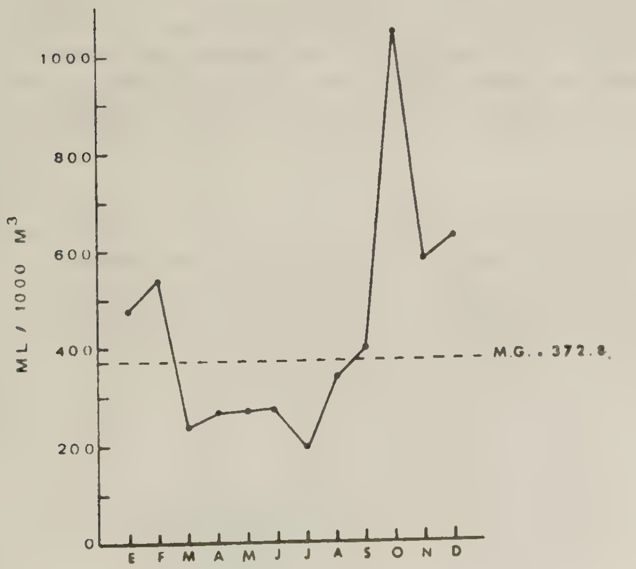


Fig. 13.- Variación estacional de la biomasa de zooplancton área I. Se grafican los valores mensuales de las medias geográficas de biomasa zooplanctónica. Las unidades son ml zooplancton /1000 metros cúbicos de agua filtrada. La media geométrica total para el período 1964-1973 se representa por una línea de trazos.

Las tres variables estudiadas, presentan una clara componente estacional. La Figura 13 muestra los promedios mensuales de la biomasa zooplanctónica en el área I. Estos promedios están expresados como medias geométricas, producto de la transformación logarítmica utilizada (la media geométrica es el anti-logaritmo del promedio artimético calculado en base a datos log-transformados). El máximo de biomasa se produce en Octubre con un valor mayor a 1000 ml/1000 m^3, equivalente a tres veces el promedio para los 10 años (372.8 ml/1000 m^3). Se observan bajas biomasas durante los meses de otoño e invierno, y un segundo máximo en verano. Este patrón bi-modal coincide con la estacionalidad de las surgencias costeras, que alcanzan en esta zona su máxima expresión durante primavera-verano.

La Figura 14A muestra los promedios mensuales de abundancia de huevos y la Figura 14B los promedios de abundancias de larvas de anchoveta *E. ringens*. Los gráficos muestran dos máximos coincidentes para huevos y larvas. El máximo principal para los huevos ocurre en Diciembre y el secundario en Julio, en cambio lo inverso ocurre con las larvas, donde el máximo principal ocurre en Julio y el secundario en Diciembre. Este patrón estacional coincide con los resultados de Simpson y Gil (1967) basados en el análisis macroscópico de los estados de madurez de las gónadas del stock desovante. La bimodalidad en el ciclo estacional del desove, se ve también reflejada en el reclutamiento a la pesquería (Simpson y Buzeta, 1967).

La Figura 15A muestra los promedios mensuales de huevos y la Figura 15B los promedios mensuales de larvas de sardina, *S. sagax*. El ciclo estacional de la abundancia de huevos muestra un máximo en Marzo, que no tiene contraparte en el gráfico de abundancia de larvas. Una inspección de los valores originales, reveló que este máximo está sesgado por un solo valor extremo y por lo tanto su validez general es dudosa. Es interesante notar, sin embargo, que tanto el porcentaje de hembras maduras, como el valor del índice gonádico para el período 1969-1977 (Serra et al., 1979), presenta un máximo en Febrero-Marzo. Esto sugiere que de haberse incorporado al presente análisis información posterior a 1973, este máximo pudiera haberse confirmado. De ser así, el desove de sardina estaría en la actualidad reproduciendo el patrón de variación estacional del desove de anchoveta.

Esto subraya el hecho que lo ocurrido en el ecosistema con posterioridad a 1972, podría ser un verdadero reemplazo ecológico, al sustituir *S. sagax* a *E. ringens* como pez filtrador dominante capaz de explotar el ecosistema en forma similar. La información reportada por Serra et al., (1979), confirma también la existencia del máximo de Septiembre, en base al muestreo del stock desovante.

En la Figura 16 se muestra la secuencia anual de gráficos mensuales de frecuencia de tallas para la pesquería de *S. sagax* de Iquique (20ºS) durante 1978 (Rojas, 1980). El reclutamiento de los juveniles a la pesquería ocurre en Enero, cuando se detectan máximos en la distribución de tallas con modas en los 9.0 y 10.7 cm. De acuerdo a la información sobre edad y crecimiento disponible (Trautman y Aguayo, 1980), estos grupos modales están en la vecindad de la longitud de peces de un año retrocalculado a partir de medición de otolitos. La longitud a la edad de un año ha sido estimada por dichos autores en 11.9 cm. En ausencia de datos experimentales sobre crecimiento temprano de *S. sagax*, esta información sugiere que el reclutamiento de Enero podría corresponder a los juveniles provenientes de los desoves tanto de Verano como de Invierno del año anterior.

Para investigar la variabilidad interanual, se seleccionó el área I, por ser la que permitía una mejor cobertura temporal del período en estudio. A las tres variables analizadas, biomasa zooplanctónica, huevos de *E. ringens* y huevos de *S. sagax*, se les eliminó el componente estacional, recalculado cada estimador mensual como la diferencia entre el valor observado y su promedio mensual. Con estos estimadores residuales se confeccionaron series de tiempo con intervalos trimestrales de acumulación.

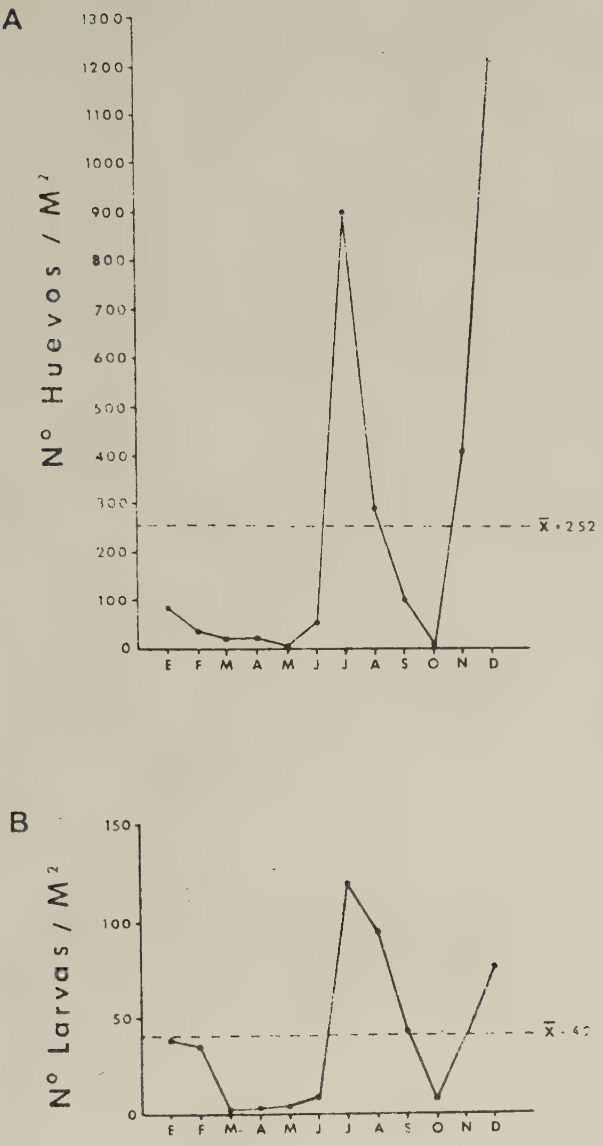


Fig. 14.- Variación estacional de huevos y larvas de anchoveta *Engraulis ringens*. A: promedios mensuales de huevos de anchoveta en área I. B: promedios mensuales de larvas de anchoveta en área I. El promedio total de la serie de datos está indicado por una línea de trazos.

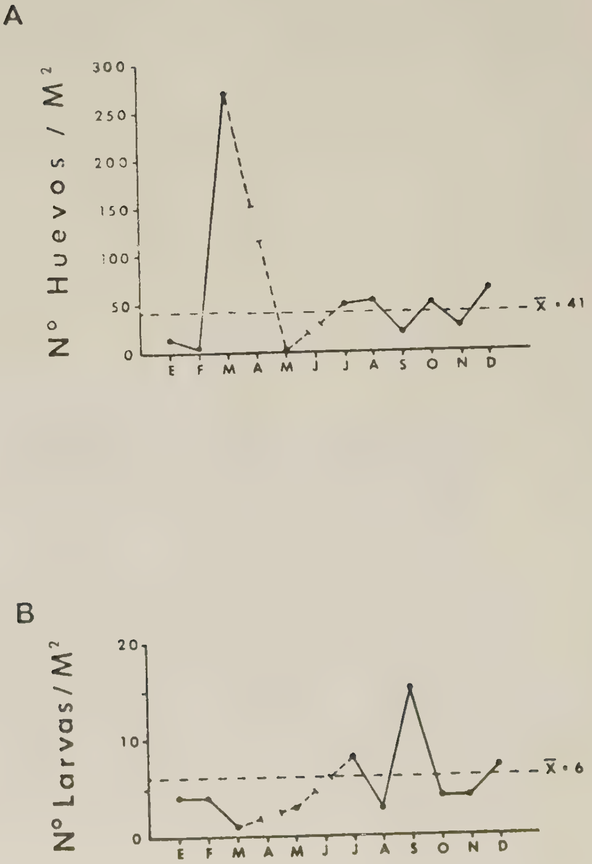


Fig. 15.- Variación estacional de huevos y larvas de sardina *S. sagax*. A: promedios mensuales de huevos de sardina en área I. B: promedios mensuales de larvas de sardina en área I. El promedio total de la serie de datos está indicado por una línea de trazos.

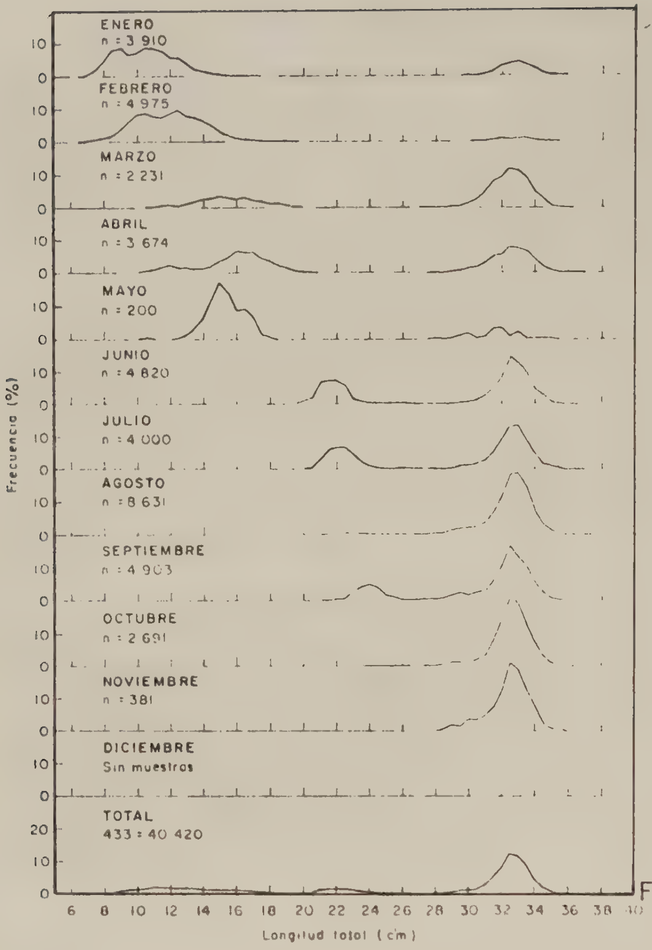


Fig.16.- Secuencia anual de distribuciones de frecuencia de tallas para la pesquería de *S. sagax* de Iquique (20ºS), durante 1978 (de Rojas, 1980).

Frecuencia de tallas [illegible] Sardinops sagax musica, 19[illegible]

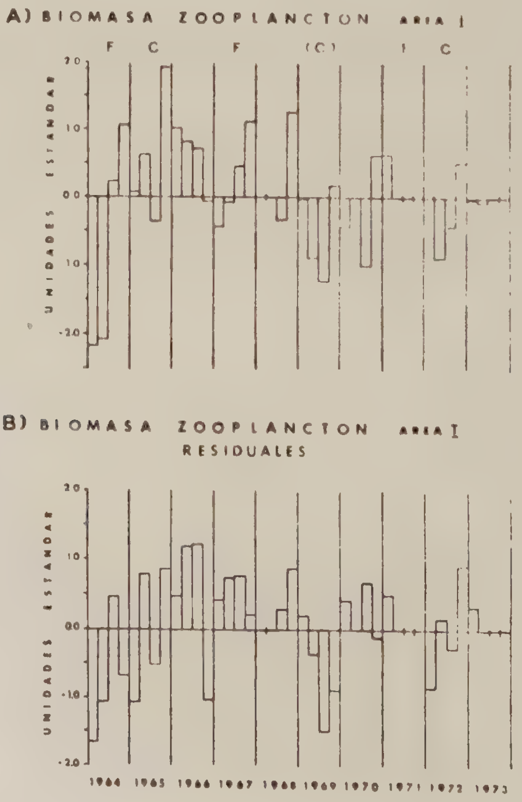


Fig. 17.- Series de tiempo de biomasa zooplanctónica área I. A: Serie de estimadores trimestrales de biomasa zooplanctónica incluyendo variación estacional. B: Serie de estimadores trimestrales de biomasa zooplanctónica. Residuales representan el componente de variación interanual. Ambas series han sido estandarizadas con sus respectivas desviaciones estándar. Los períodos fríos y cálidos están indicados por las letras F y C respectivamente.

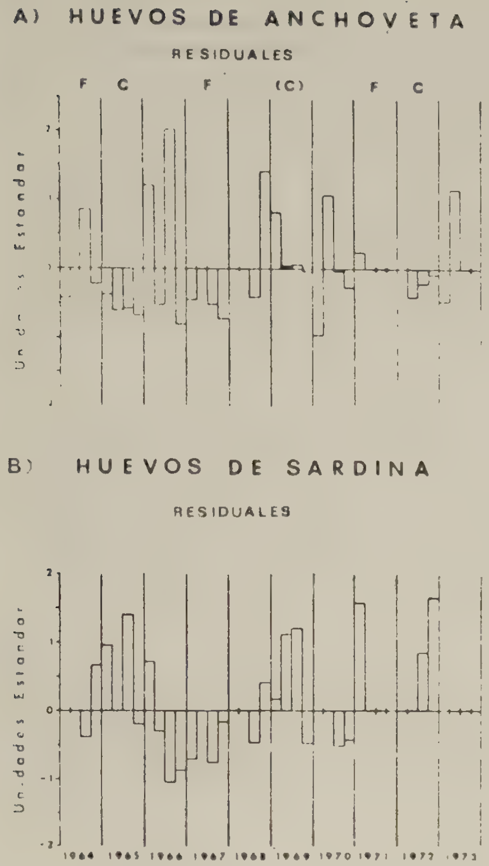


Fig. 18.- Series de tiempo de huevos de anchoveta *E. ringens* y de sardina *S. sagax* área I.
A: Serie de estimadores trimestrales residuales de huevos de anchoveta representativos del componente de variación interanual.
B: Serie de estimadores trimestrales residuales de huevos de sardina representativos del componente de variación interanual.
Ambas series han sido estandarizadas con sus respectivas desviaciones estándar.
Los períodos fríos y cálidos están indicados por las letras F y C respectivamente.

La Tabla 3 compara las fracciones de la variabilidad total de las series de tiempo, asociadas al ciclo estacional y las series residuales. Estos porcentajes de varianza fueron calculados por diferencia entre las sumas de cuadrados de las series mensuales sin modificarlas (varianza total), menos la suma de cuadrados de las series mensuales de residuales (varianza interanual). La diferencia de ambas sumas de cuadrados es precisamente el componente estacional.

Tabla 3.- PROPORCION DE LA VARIABILIDAD TOTAL 1964-1973 ASOCIADA AL CICLO ESTACIONAL
AREA DE ACUMULACION I: 18°-24°L.S.

	Estacional	Largo período	N
Biomasa zooplancton	49.0%	51.0%	50
Huevos *Engraulis ringens*	29.7%	70.3%	54
Huevos *Sardinops sagax*	39.2%	60.8%	43

Los resultados de este análisis indican que la variabilidad total de la biomasa está distribuida en forma equitativa entre el componente estacional y el de largo período (o baja frecuencia). Este resultado contrasta notoriamente con la situación existente en la Corriente de California, donde en promedio sólo el 18% de la varianza total está asociada a la señal estacional. Debe tenerse en cuenta, como se comenta más adelante, que las distintas metodologías utilizadas en ambos casos para la obtención de las muestras en terreno no son estrictamente comparables.

En las series de tiempo de abundancia de huevos, tanto de *E. ringens* como de *S. sagax*, sólo alrededor de un tercio de la varianza total está asociada al ciclo estacional y los dos tercios restantes a fluctuaciones de largo período interanuales. Esto permite sugerir que los stocks de peces pelágicos pudieran ser afectados en forma más directa que el zooplancton, por las alteraciones del régimen oceanográfico asociadas a los períodos fríos y cálidos.

Atendiendo a que de las tres series de tiempo una de ellas tiene unidades distintas, y a que entre las dos series de huevos, sus valores absolutos son muy diferentes, las series fueron estandarizadas respecto a sus propias varianzas. Con este fin, cada valor mensual fue escalado respecto a la desviación estándar mensual de la serie. Es así como un valor de +/-1.0, significa un valor mensual de la variable equivalente a una desviación estándar por sobre o bajo su promedio mensual.

La Figura 17A muestra la serie de tiempo de biomasa trimestrales y la Figura 17B la serie de residuales de biomasa. En 1964 se observan los valores más bajos de las series, coincidentes con un período anómalo frío (F en la Figura 17). Durante el período cálido de 1965 (El Niño), no se detecta una disminución de la biomasa en ambas series, por el contrario, estas presentan desviaciones positivas respecto al promedio. En general, se puede concluir que no existe una relación consistente con la respuesta esperada del ecosistema a las perturbaciones, es decir un aumento de la biomasa durante un período frío y una disminución durante un período cálido.

La información existente presenta algunas limitaciones respecto a la representatividad de las muestras de zooplancton. La capa muestreada abarca sólo los 50 m superficiales y por lo tanto, una importante fracción del zooplancton epipelágico ha quedado excluido del muestreo. La red de Hensen utilizada en arrastres verticales, aunque adecuada para censos de huevos de peces, no es particularmente apropiada para la captura de los miembros más móviles del zooplancton (por ejemplo, eufáusidos, quetognatos, e incluso algunos grupos de copépodos). Una diferencia importante, entre los datos de California y los de Chile-Perú, es la extensión fuera de la costa del área muestreada. El estudio de la variabilidad biológica en California utilizó información colectada hasta 550 Km fuera de la costa, en cambio en Chile-Perú las áreas de acumulación abarcan sólo hasta 56 Km fuera de la costa. El carácter costero del muestreo en el Pacífico sur, lo hace poco adecuado para investigar fenómenos de gran escala, los que a juzgar por lo que se conoce de California, se originan en gran medida en respuesta a variaciones del flujo de todo el Sistema de Corrientes. Un muestreo biológico representativo con este fin, debiera por lo menos abarcar hasta el borde externo de la Corriente de Humboldt (ver Figura 3).

Sin embargo, estos sesgos de muestreo se mantuvieron constantes a lo largo de todo el período, y las conclusiones que se derivan son consistentes entre sí. Por lo tanto, cabe concluir que posiblemente los cambios de abundancia de zooplancton, en la faja costera entre 18ºy 24ºS, no están estrechamente conectados a los efectos producidos por períodos anómalos fríos o cálidos.

La Figura 18 presenta las series de tiempo de los residuales de abundancia de huevos de anchoveta (18A) y sardina (18B). En ellas, el período cálido de 1965 muestra anomalías negativas en el caso de la anchoveta y positivas para la sardina. En 1969, otro período cálido, la anchoveta muestra sólo en el primer trimestre valores positivos significativos y el resto del año valores muy cercanos al promedio; en cambio la sardina vuelve a presentar anomalías positivas importantes. Durante 1972, el tercer período cálido de la serie, se vuelve a repetir el caso de 1965, con anomalías negativas de la anchoveta y positivas de la sardina. Es una observación relevante que esta relación inversa entre *E. ringens* y *S. sagax* se haya presentado en forma consistente en los tres períodos cálidos de la serie. Sin embargo, no existe una tendencia clara en la respuesta de cada especie, o de ambas, respecto a la secuencia de períodos fríos y cálidos. Por ejemplo 1967, un período frío contra lo esperado, presenta para ambas especies anomalías negativas.

La relación inversa en la intensidad del desove de ambas especies durante los períodos cálidos, es quizás el resultado más interesante de este análisis preliminar de los datos históricos de la región. Es evidente que esta respuesta inversa, no es suficiente por sí sóla para desencadenar una secuencia de reemplazo de una especie por otra, ya que de ser así, esto habría tenido lugar en 1965 o 1969. Al respecto debe recordarse que los residuales no representan abundancias absolutas, y que las abundancias de huevos de anchoveta fueron siempre mayores, durante el período. Un segundo aspecto a considerar, es que las series representan la variación del desove, es decir, solo la primera etapa del proceso que culmina en la génesis de una nueva clase anual en la población, y que en el mejor de los casos, el desove serviría para estimar el tamaño del stock desovante, pero en ningún caso es un buen índice del éxito de la clase anual siguiente. Precisamente, gran parte de los mecanismos tanto ambientales como biológicos, que determinan el éxito de una clase anual, actúan entre el desove y el reclutamiento de los juveniles al stock reproductor. Una comparación de estas series de tiempo con series de tiempo del reclutamiento en el mismo período es un objetivo altamente pertinente.

Es razonable esperar que los cambios en la dinámica y distribución de las masas de agua del Sistema en respuesta a condiciones anómalas, tengan consecuencias biológicas inmediatas respecto a las condiciones y estructura espacial del hábitat de las especies pelágicas.

Aunque hasta el momento no se conocen los mecanismos involucrados, es posible suponer que en el necton tengan lugar desplazamientos poblacionales importantes, en respuesta a la redistribución de las masas de aguas. Por otra parte, las poblaciones planctónicas, debido a su menor capacidad de movimiento, pueden experimentar un deterioro de su hábitat localmente, con mortalidades naturales anómalamente elevadas. El desplazamiento de especies nectónicas, aunque pudiera significar el alivio de presiones ambientales negativas para las subpoblaciones adultas, puede significar el franco deterioro del ambiente para sus estadios larvales, en general mucho más sensibles a la calidad del ambiente. Salinidades, temperaturas, niveles de turbulencia y estratificación levemente distintos pueden ser letales para las larvas, ya sea en forma directa o alterando la disponibilidad (concentración) y calidad (composición y tamaño) del alimento larval. Elevadas mortalidades larvales, después de un desove exitoso, pueden ser igualmente efectivas para limitar el reclutamiento y éxito de la clase anual siguiente.

Agradecimientos

Deseamos expresar nuestros agradecimientos al Ingeniero Roberto Cabezas Bello, Director Ejecutivo y al Sr. Alfredo Sanhueza Seguel, Jefe de la División de Recursos de IFOP por las facilidades entregadas a los autores para la realización de este trabajo. La División de Investigación de la Sede Regional Talcahuano de la Pontificia Universidad Católica de Chile hizo posible el procesamiento de la información de biomasa y huevos y larvas de peces, otorgando el financiamiento necesario. Agradecemos también a la Srta. Teresa Fierro, por su ayuda con las ilustraciones y a las Srtas. Liliana Lagos y Eliana Figueroa quienes dactilografiaron el manuscrito. La presentación de este trabajo en San José de Costa Rica ha sido posible gracias al financiamiento generoso otorgado por la Comisión Oceanográfica Intergubernamental.

REFERENCIAS

Antezana-Jerez, T. 1978. Distribution of Euphausiids in the Chile-Perú Current with particular reference to the endemic Euphausia mucronata and the oxygen minima layer. Ph.D. Dissertation Scripps Institution of Oceanography, University of California San Diego.

Bakun, A. y R.H. Parrish. 1982. Turbulence, transport and pelagic fish in the California and Perú current system. CALCOFI Rep. (23):99-112.

Bernal, P.A. 1979. Large-scale biological events in the California Current. CALCOFI Rep. (20):89-101.

__________. 1980. Large-scale biological events in the California Current: the low-frequency response of the epipelagic ecosystem. Ph.D. Dissertation Scripps Institution of Oceanography, University of California San Diego.

__________. 1981. A review of the low-frequency response of the pelagic ecosystem in the California Current. CALCOFI Rep. (22):49-62.

Brockmann, C., E. Fahrbach, H. Huyer y R.L. Smith. 1980. The poleward undercurrent along the Perú coast: 5-15º. Deep-Sea Res. (27A):847-856.

Cañón, J.R.C. 1980. Prognosis del ambiente físico de las pesquerías chilenas. Informe del Programa "Perspectivas de desarrollo de las pesquerías nacionales", Corporación de Fomento de la Producción - Gerencia de Desarrollo. Instituto de Fomento Pesquero - Chile. Ref: AP 80-3:152 pp.

Chelton, D.B. 1980. Low frequency sea level variability along the west coast of North America. Ph.D. Dissertation Scripps Institution of Oceanography, University of California San Diego.

__________. 1981. Interannual variability of the California Current: physical factors. CALCOFI Rep. (22):34-48.

Chelton, D.B., P.A. Bernal y J.A. McGowan. 1982. Large scale interannual physical and biological interaction in the California Current. J.Mar.Res. 40(4):1095-1125.

Enfield, D.B. 1981. Annual and nonseasonal variability of the monthly low-level wind fields over the Southeastern Tropical Pacific. Monthly Weather Rev. 109(10):2177-2190.

Enfield, D.B. y J.S. Allen. 1980. On the structure and dynamic of monthly mean sea level anomalies along the Pacific coast of North and South America. J.Physical Oceanogr. 10(4):557-578.

Johnson, D.R., T. Fonseca y H. Sievers. 1980. Upwelling in the Humboldt Coastal Current near Valparaíso, Chile. J.Mar.Res. 38(1):1-16.

Kramer, D. 1970. Distributional atlas of fish eggs and larvae in the California Current region: Pacific sardine, Sardinops caerulea (Girard), 1951 through 1966. CALCOFI Atlas No.12, vi pp, 277 charts.

Kramer, D. y E.H. Ahlstrom. 1968. Distributional atlas of fish larvae in the California Current region: northern anchovy, Engraulis mordax Girard, 1951 through 1965. CALCOFI Atlas No.9, xi pp, 269 charts.

McCreary, J. 1976. Eastern Tropical Ocean response to changing wind systems: with application to El Niño. J.Physical Oceanogr. 6:632-645.

McGowan, J.A. 1974. The nature of oceanic ecosystems. pp. 9-28. In The biology of the Oceanic Pacific, (C.B. Miller, ed.). Oregon State University Press, Corvallis.

Miller, F.R. y R.M. Laurs. 1975. The El Niño of 1972-1973 in the Eastern Tropical Pacific Ocean. Bull.Inter-Amer.Trop.Tuna Comm. 16(5):403-408.

Parrish, R.H. y A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. California Dept. Fish and Game, Fish Bull. 167:1-110.

Quinn, W.H. 1974a. Monitoring and predicting El Niño invasions. J.Applied Meteorology. 13(7):825-830.

__________. 1974b. Outlook for El Niño-type conditions in 1975. School of Oceanography Oregon State University, Corvallis (mimeo).

Robles, F.L. 1979. Water masses and circulation in the South-East Pacific and the El Niño event. Ph.D. Dissertation, Department of Oceanography, University of Wales, U.K. 2 vols:175 and 156 pp.

Robles, F.L., E. Alarcón y A. Ulloa. 1980. Water masses in the northern Chilean zone and their variations in the cold period (1967) and warm periods (1969, 1971-73). pp. 83-174. In Proceedings of the Workshop on the Phenomenon known as El Niño. UNESCO, Paris.

Rojas, O. 1980. Estructura poblacional de la sardina española (Sardinops sagax musica) en la zona norte de Chile. En Informe del programa: "Investigaciones del recurso sardina española (Sardinops sagax)", Corporación de Fomento a la producción-Gerencia de desarrollo. Instituto de Fomento Pesquero - Chile. Ref: AP 80-5:1-18.

Ryther, J.H., D.W. Menzel, E.M. Hulburt, C.J. Lorenzen y N. Corwin. 1971. The production and utilization of organic matter in the Peru Coastal Current. Investigaciones Pesqueras (Barcelona). 35:43-60.

Santander, H. y O.S. de Castillo. 1977. Variaciones en al intensidad del desove de la sardina Sardinops sagax sagax (J.) en la costa peruana en los años 1966-1973. Bol.Inst.Mar Perú. 3(3):73-94.

Serra, J.R., M. Aguayo, O. Rojas, J.R. Cañón y F. Inostroza. 1979. Anchoveta Engraulis ringens Jenyns, Teleostomi, Clupeiformes, Engraulidae. En "Estado actual de las principales pesquerías nacionales. Peces." Corporación de Fomento de la Producción-Gerencia de desarrollo. Instituto de Fomento Pesquero - Chile. Ref: AP 79-78:52 pp.

Silva, N. y H. Sievers. 1981. Masas de agua y circulación en la región de la rama costera de la Corriente de Humboldt, latitudes 18ºS - 33ºS (Operación Oceanográfica MARCHILE 10-ERFEN 1). Ciencia y Tecnología Marinas, Comité Oceanográfico Nacional (Chile) 5:5-50.

Simpson, J.G. y R. Buzeta. 1967. El crecimiento y la edad de la anchoveta (Engraulis ringens, Jenyns) en Chile basado en estudios de frecuencia de longitudes. Bol.Cient.Inst.Fom.Pesq., Santiago-Chile. 3:1-53.

Simpson, J.G. y E. Gil. 1967. Maduración y desove de la anchoveta (Engraulis ringens) en Chile. Bol.Cient.Inst.Fom.Pesq., Santiago-Chile. 4:1-55.

SIO-WHOI-MIT. 1969. Physical and chemical data from the Scorpio Expedition in the South Pacific Ocean. USNS Eltanin, Cruises 28 and 29, 1967. Scripps Institution of Oceanography - Woods Hole Oceanographic Institution and Massachussetts Institute of Technology. SIO Reference 69-15, WHOI Reference 69-56, 89 pp.

Trautman, S. y M. Aguayo. 1980. Edad y crecimiento de sardina española (Sardinops sagax musica). En Informe del Programa: "Investigaciones del recurso sardina española (Sardinops sagax)", Corporación de Fomento a la Producción-Gerencia de desarrollo. Inst.Fom.Pesq., Chile. Ref: AP 80-5:1-24.

Wyrtki, K. 1967. Circulation and water masses in the Eastern Equatorial Pacific Ocean. International Journal Oceanology and Limnology. 1(12):117-147.

Zuta, S., D.B. Enfield, J. Valdivia, P. Lagos y C. Blandin. 1980. Physical aspects of the 1972-73 El Niño phenomenon. pp. 11-62. In Proceedings of the Workshop on the Phenomenn known as El Niño. UNESCO, Paris.

VARIABILIDAD BIOLOGICA DE BAJA FRECUENCIA Y GRAN ESCALA EN LA CORRIENTE DE CALIFORNIA, 1949-1978

Por

P.A. Bernal
BIOTECMAR
Pontificia Universidad Católica de Chile
Sede Regional Talcahuano
Casilla 127 - Talcahuano, Chile

y

D.B. Chelton
Jet Propulsion Laboratory
California Institute of Technology
Pasadena, California 91109
USA

Summary

The pelagic ecosystems of the California Current shows biological responses dominated by large scale, low frequency changes. These fluctuations are not associated with the coastal water movements. On the contrary, this study shows that they are strongly associated with inter-annual fluctuations of the transport of the California Current.

Zooplankton biomass time series were strongly correlated with the temperature field ($r= 0.77$; $p < 0.05$). This indicated that horizontal and vertical advection play primary roles in these changes. The biomass fluctuations are most highly correlated with current transport five months prior to the changes ($r=0.77$; $p<0.05$). At the same time, these changes are associated with fluctuations of thermal anomalies in the eastern tropical Pacific indicative of "El Niño" events ($r=0.74$; $p<0.05$), with a 4 month lag.

Density independent factors controlling populations in eastern boundary currents are discussed, emphasizing the importance of incorporating parameter estimations for the oceanographic fluctuations in fishery management models. The relation between anomalous changes in California Current transport and sea level observation time series from coastal tide-gauge measurements. For the northern hemisphere there is a highly significant relation with rising coastal sea level preceding the transport anomalies ($r=0.83$; $p<0.05$).

INTRODUCCION

Las corrientes de márgen oriental de los giros subtropicales, han sido reconocidas desde temprano, como entre las más productivas de los océanos. Los niveles de producción primaria observados en ellas, son uno o dos órdenes de magnitud superiores a los observados en otros ecosistemas oceánicos. Por ejemplo, en Perú Ryther et al., (1971) reportan niveles de 11.7 gr-C m^{-2} d^{-1}, en cambio para el ecosistema del giro central del Pacífico Norte, Venrick et al. (1973) citan valores típicos entre 0.1 a 0.2 gr-C $m^2 d^{-1}$. Esta elevada producción biológica se debe a las altas tasas de incorporación de nutrientes inorgánicos (fosfatos y nitratos) a las capas superficiales produciendo altos niveles de fitoplancton. Como el fitoplancton es la fuente alimenticia principal del zooplancton herbívoro, y este a su vez sirve de alimento para muchos peces pelágicos, existe un correspondiente de alta productividad en los niveles superiores de la cadena trófica.

En contraste con los ecosistemas oceánicos localizados en los giros centrales de los océanos, los ecosistemas de los sistemas de márgen oriental, además de estar abiertos a flujos de masa y energía canalizados directamente hacia la producción orgánica, están también abiertos a la entrada a gran escala de energía mecánica en la forma de advección horizontal y del forzamiento local de los vientos. Estos sistemas se caracterizan biológicamente, tanto por presentar una elevada heterogeneidad espacial de las poblaciones planctónicas residentes (Haury, 1976), como por exhibir una predictibilidad temporal reducida (Hayward y McGowan, 1979).

Para estos sistemas, se ha propuesto que a causa de los efectos disruptivos de las condiciones físicas en estas regiones, los mecanismos clásicos de interacción biológica (competencia y predacción), pueden no tener la oportunidad de jugar un rol dominante en el control de la composición de especies, ni en la modulación de sus cambios de abundancia (McGowan, 1974). Estudios de las fluctuaciones de biomasa planctónica en la Corriente de California entre 1955 y 1959, proveen evidencias en apoyo de esta hipótesis. Por ejemplo, la biomasa de copépodos, que en promedio corresponde a un tercio de la biomasa total, entre Octubre de 1955 y Octubre de 1958 disminuyó un orden de magnitud desde 44.8 gm / 1000 m^3 a 4.1 gm / 1000 m^3. Se ha calculado que este cambio es equivalente a un flujo de energía de 4 x 10^{12} watts en la Corriente de California. Colebrook (1977) utilizando análisis de componentes principales, demostró cambios de abundancia sorprendentemente coherentes tanto entre los 17 taxa analizados, como entre diferentes localidades. Estudios de sedimentos finamente estratificados provenientes de fosas anaeróbicas frente a las costas de California, indican que grandes fluctuaciones en las abundancias de peces y componentes del zooplancton, han tenido lugar en forma regular durante los últimos 200 años (Soutar e Isaacs, 1969 y 1974).

Aunque el aumento en número de algunos taxa a expensas de otros podría ser explicada en base a interacciones biológicas, dicha explicación se hace insostenible cuando la mayoría de los taxa tiende a aumentar (o disminuír) simultáneamente en gran parte del ecosistema. Considerando que las escalas temporales de los fenómenos demográficos relevantes para el fito y zooplancton son mucho más cortas que la escala de variación típica de los cambios observados en los sedimentos; y que Colebrook en su estudio documentó el cambio simultáneo en la abundancia de 17 taxa distintos; es razonablemente concluir que las condiciones ambientales de gran escala juegan un rol mucho más significativo que la competencia y predación en el control de la biomasa en la Corriente de California.

Para las corrientes de márgen oriental generalmente se acepta que el proceso principal responsable de la incorporación de nutrientes inorgánicos de origen no-regenerativo (y por lo tanto responsable de la "producción nueva") es la surgencia costera. Si las surgencias costeras fueran responsables de la producción primaria, e indirectamente de la producción del zooplanton en estos sistemas, se debiera esperar que el máximo de biomasa observado se encontrará adyacente a la línea de costa, o por lo menos dentro de un radio de deformación de Rossby. Dos evidencias contradicen esta suposición. Primero, la zona enriquecida biológicamente en California es un orden de magnitud más ancha que un radio de deformación de Rossby. Segundo, el máximo de biomasa zooplanctónica observado se ubica entre 100-150 Km de la costa (figura 1) lo que se ve confirmado por la distribución de biomasa observada en cortes frente a San Francisco (figura 2a) y Los Angeles (figura 2b). Aunque las surgencias costeras indudablemente juegan un papel importante en forma local, es evidente que otros procesos deben ser responsables, a lo menos en parte, de las características biológicas de gran escala.

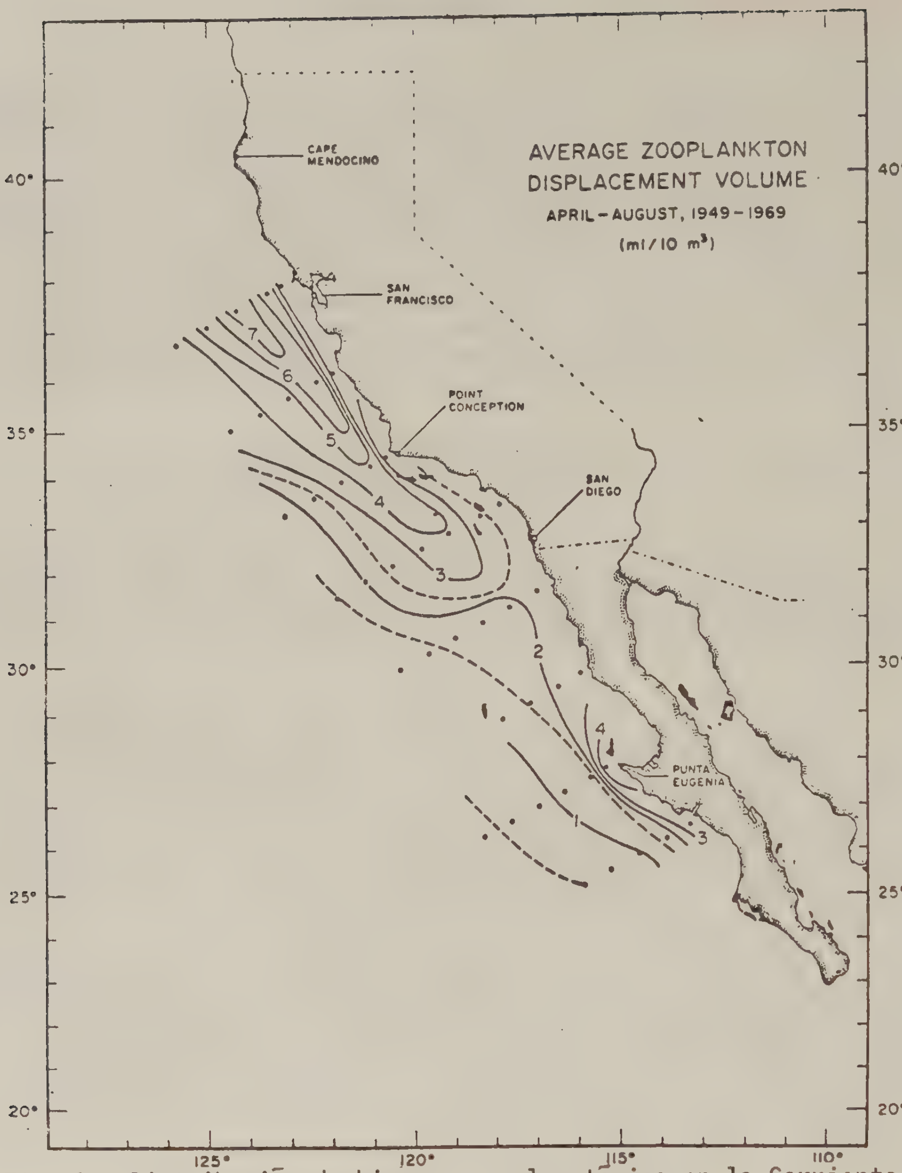

AVERAGE ZOOPLANKTON
DISPLACEMENT VOLUME
APRIL - AUGUST, 1949 - 1969
(ml/10 m³)
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
7
6
5
4
3
2
1
4
3
40°
35°
30°
25°
20°
125°
120°
115°
110°

Fig. 1.- Distribución de biomasa zooplanctónica en la Corriente de California. Promedios 1949-1978.

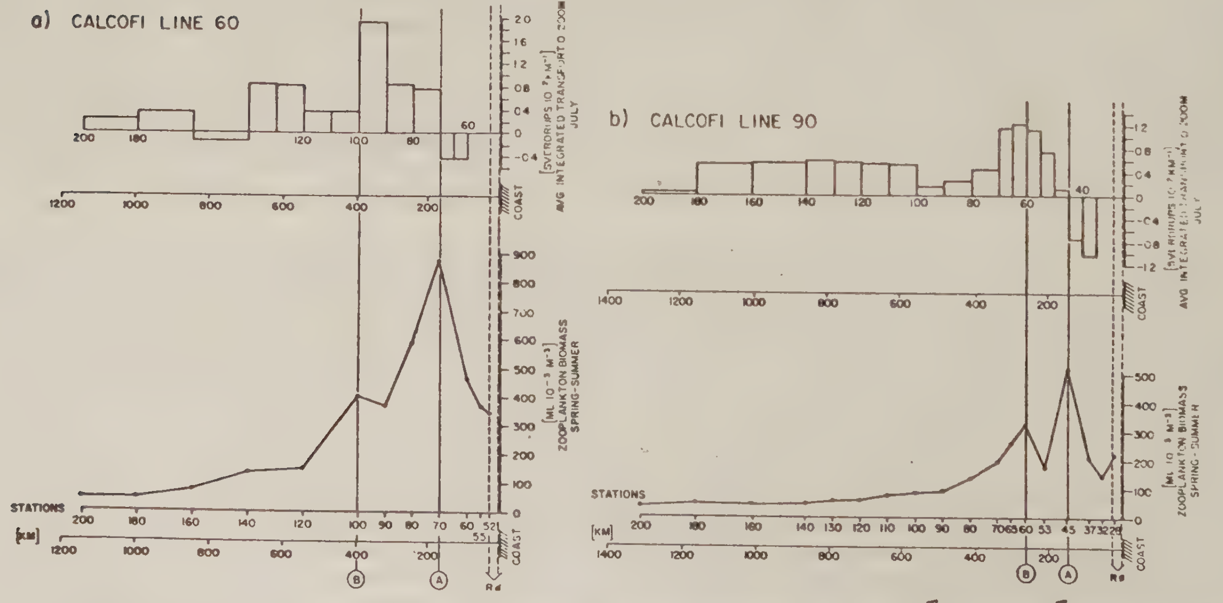


Fig. 2 (a) Transporte geostrófico y promedios de biomasa zooplanctónica. Línea CalCOFI 60 y (b) Transporte geostrófico y promeidos de biomasa zooplanctónica. Línea CalCOFI 90.

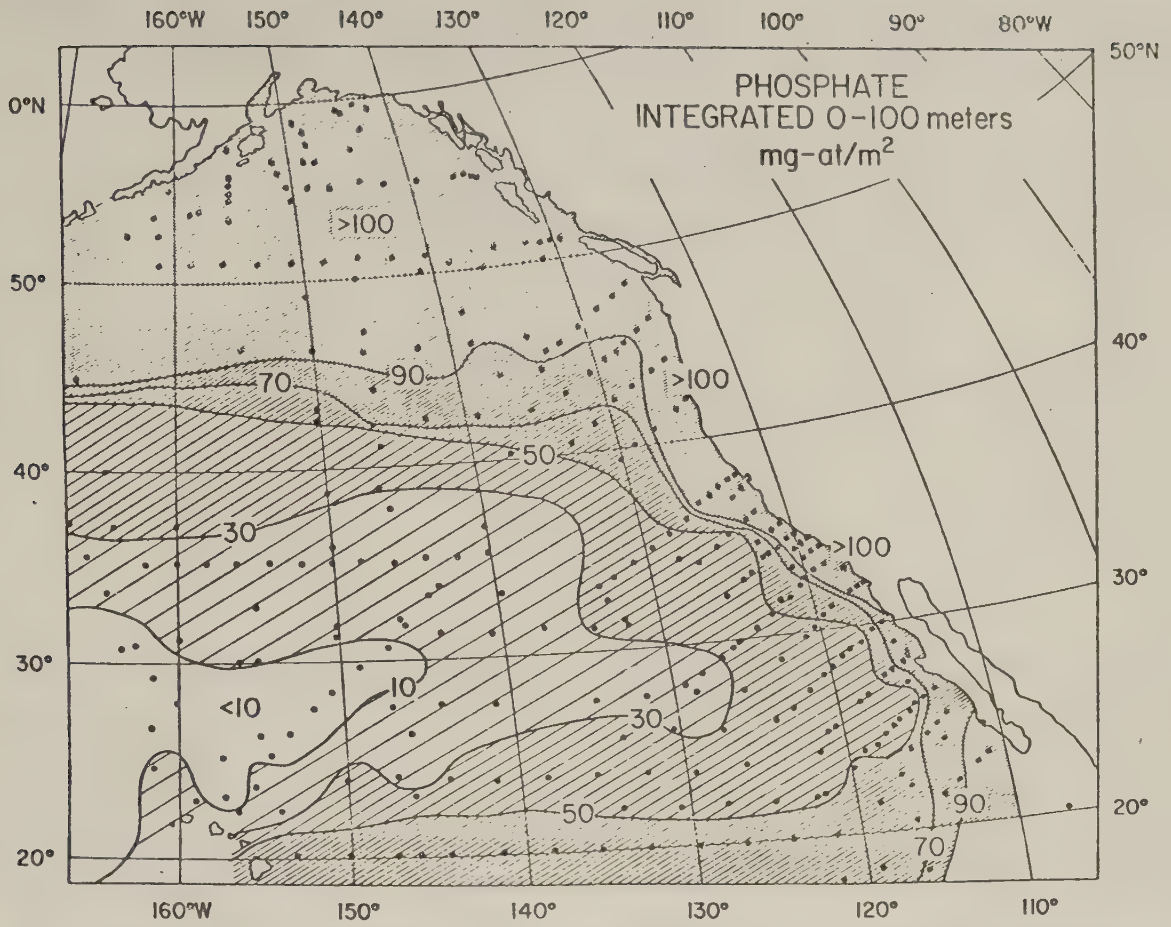


Fig. 3.- Distribución de fosfatos en el Pacífico Norte. Valores integrados desde 100 m hasta la superficie. Unidades mg-at/m^2.

Tanto en el hemisferio Norte como en el Sur, los ecosistemas de márgen oriental se encuentran "corriente abajo" de sistemas oceánicos con altos niveles de nutrientes. La figura 3 muestra la distribución de fosfatos en el Pacífico Norte. La penetración hacia el sur de extensiones tanto en la distribución de biomasa como en la de fosfatos, enfatiza la importancia que tiene la advección horizontal de gran escala para la producción de estos sistemas. Reid (1962) propuso por primera vez la existencia de una relación entre advección y zooplanton en California. Wickett (1967) encontró una relación entre la biomasa de zooplancton en California y el forzamiento de los vientos superficiales en el giro de Alaska un año antes. Wickett sugirió que el zooplancton estaría respondiendo al mayor contenido de nutrientes de las aguas de la divergencia de Alaska que habrían sido transportadas por advección hacia el sur. Bernal (1980) y Bernal y McGowan (1981) presentaron evidencia relacionando el transporte geostrófico de origen subártico con la abundancia de zooplancton.

El própósito de esta presentación es dar cuenta de los resultados de diversas investigaciones que demuestran la existencia de fluctuaciones de baja frecuencia en la respuesta del ecosistema pelágico, en la Corriente de California, y examinar la relación que existe entre estas variaciones y las variaciones del medio ambiente físico.

CARACTERIZACION DE LA VARIABILIDAD BIOLÓGICA INTERANUAL EN LA CORRIENTE DE CALIFORNIA

Con el fin de analizar la variabilidad biológica en la Corriente de California, a partir de la base de datos acumulados entre 1949 y 1969 por el programa CalCOFI (California Cooperative Oceanic Fisheries Investigations) se derivaron cuatro series de tiempo de la biomasa de macrozooplancton. Los datos originales provienen de arrastres oblícuos de plancton en los 140 m superficiales con una red de 0.78 m^2 de boca equipada con una malla filtrante de 5 m de largo y 0.505 mm de trama. La figura 4 muestra la distribución de las estaciones y los límites de las áreas geográficas de acumulación estadística. En cada área se utilizó como estimador mensual de la biomasa, el promedio de los volúmenes de plancton previamente $\log_e$ transformados. En la figura 4 $\bar{n}$ representa el número típico de observaciones incluidas en los promedios mensuales.

La Tabla 1 muestra una partición de la varianza total de las series en un componente estacional y uno residual de largo período. La estacionalidad da cuenta de un máximo de 30% de la variabilidad en el área I, y de un mínimo de 8.4% en el área III.

TABLA 1

PROPORCION DE LA VARIABILIDAD TOTAL 1949-1969 ASOCIADA AL CICLO ESTACIONAL EN CORRIENTE CALIFORNIA

	ESTACIONAL	**LARGO PERIODO**
AREA I	30.0	70.0
AREA II	22.7	77.3
AREA III	8.4	91.6
AREA IV	13.6	86.4

Como el interés fundamental en este estudio son las variaciones de largo período, y atendiendo que el componente estacional representa en promedio alrededor del 18% de la varianza total, se procedió a eliminar la estacionalidad de las series. Por esto, cada valor observado se redefinió como una desviación respecto a su promedio mensual calculado sobre todo el período de estudio. Las series presentan distintas varianzas totales en términos absolutos, por esto con el fin de facilitar las intercomparaciones, cada valor fue también escalado respecto a la desviación estándar del área respectiva. Este tratamiento de los datos hace que los elementos mensuales que componen las series representen anomalías de biomasa con promedio 0 y desviación estándar 1. En la figura 5 se muestran las series para las cuatro áreas. Una simple inspección de los patrones de variación muestra que existe co-variación entre las áreas y que algunos eventos son comunes a dos o más de ellas.

La escala de tiempo característica de estas series es larga. La figura 6 muestra las funciones de autocorrelación calculadas para las cuatro áreas. La área I muestra la escala de tiempo más corta, 14 meses, y la área IV la más larga, 24 meses. Las áreas II y III muestran escalas de tiempo intermedias de 18 meses. En comparación la escala de tiempo característica del forzamiento de los vientos sobre la región es mucho más corta, alrededor de 1 mes.

Del cómputo del espectro de varianza para las cuatro series, resulta aparente que gran parte de la varianza total está asociada a fluctuaciones en la banda de baja frecuencia. La coherencia entre estos espectra es también significativa en las bajas frecuencias (Bernal, 1979). Los porcentajes de varianza asociados a distintas bandas espectrales indican que alrededor de un 50% de la varianza total está asociado a fluctuaciones de frecuencias menores a 0.05 ciclos mes^{-1}, lo que equivale a decir que las fluctuaciones dominantes en las series presentan períodos característicos de 20 o más meses. Estos resultados contrastan notoriamente con las hipótesis propuestas por Walsh (1977) para el espectro de forzamiento de la respuesta biológica en ecosistemas de margen oriental. Este autor propone la existencia de un amplio máximo espectral entre 0.016 y 0.060 ciclos día^{-1} para el zooplancton, sin embargo, en California el zooplancton estaría respondiendo a un forzamiento con un máximo espectral en frecuencias menores a 0.0016 ciclos día^{-1}, un orden de magnitud inferior a lo propuesto.

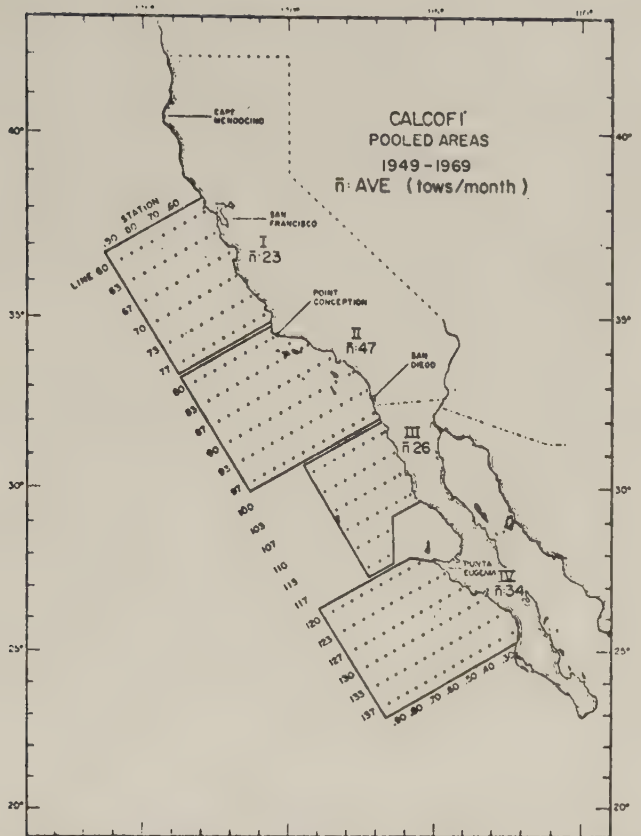

CALCOFI
POOLED AREAS
1949 - 1969
n̄: AVE (tows/month)
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
STATION
LINE
I n̄:23
II n̄:47
III n̄:26
IV n̄:34
40°
35°
30°
25°
20°

Fig. 4.- Areas de acumulación estadística para las series de tiempo de biomasa zooplanctónica "n" indica el número típico de observaciones mensuales incluidas en un promedio.

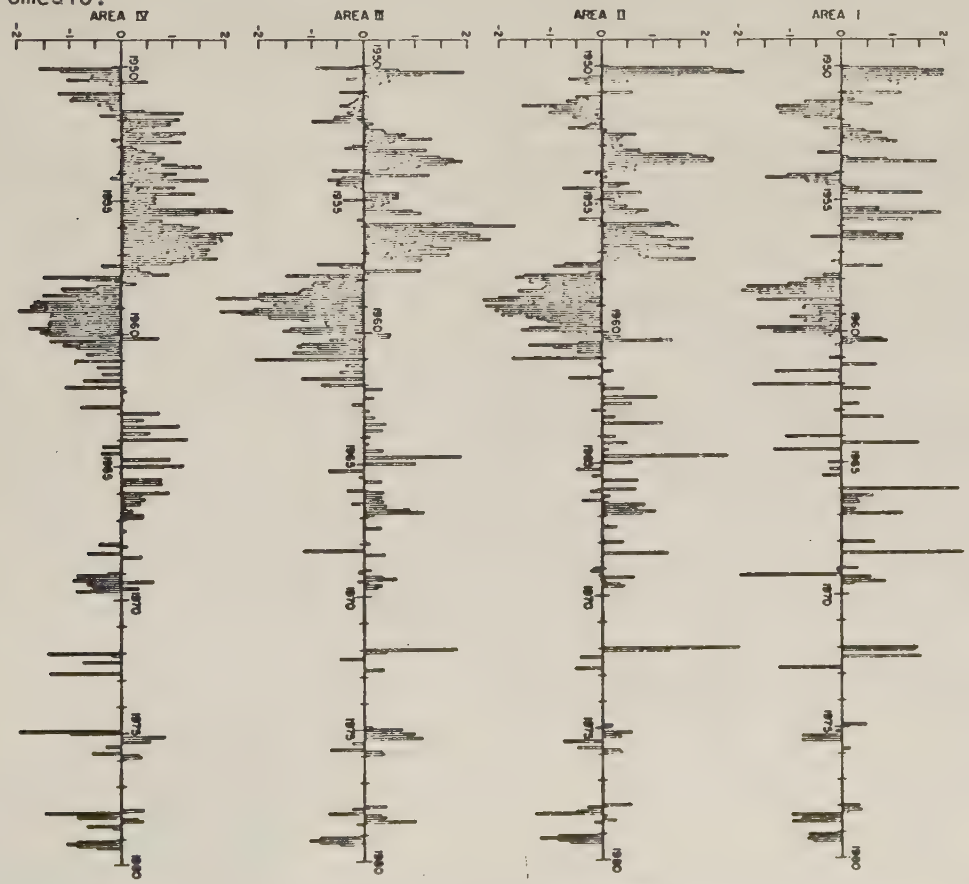


Fig. 5.- Series de tiempo de biomasa zooplanctónica para las cuatro áreas de acumulación. Cada valor es la desviación del promedio mensual respectivo escalado por su correspondiente desviación estándar. Cada serie tiene promedio cero y desviación estándar unitaria.

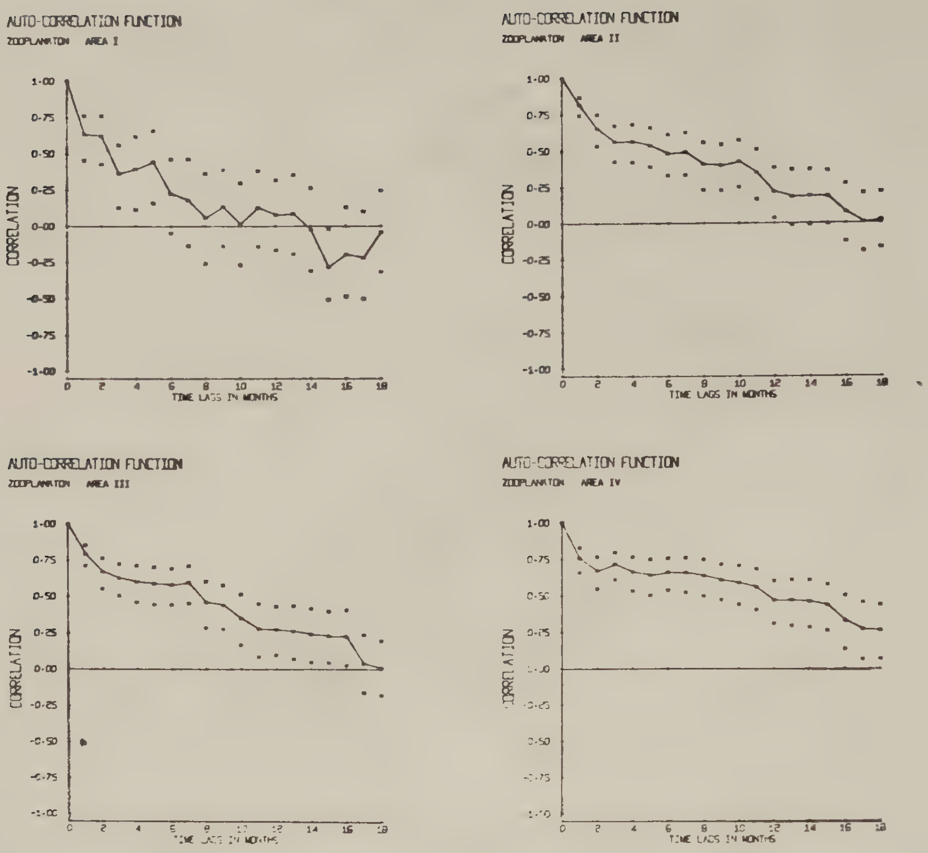


Fig. 6.- Funciones de autocorrelación de biomasa zooplanctónica.

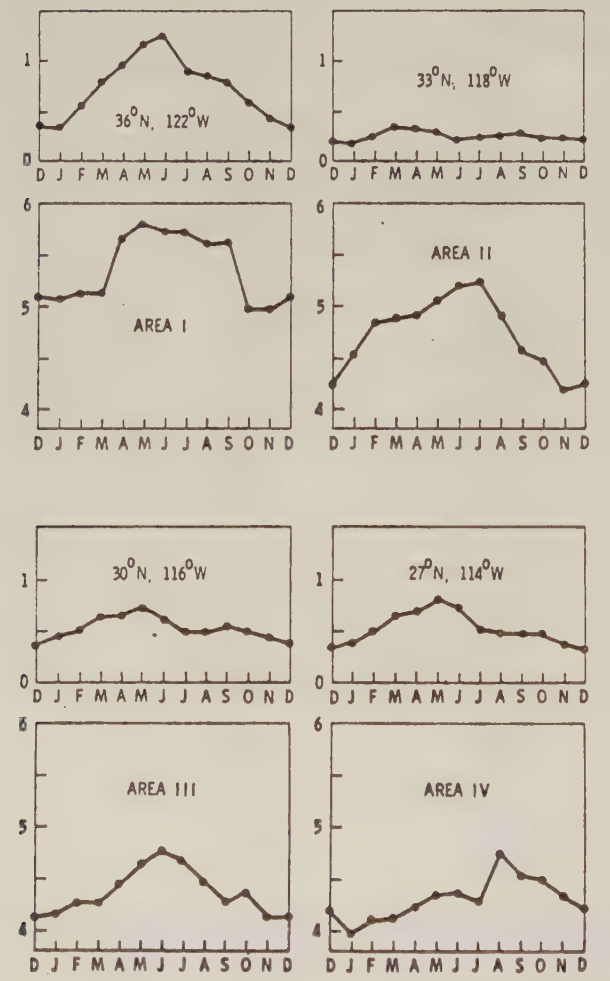


Fig. 7.- Ciclos estacionales de biomasa zooplanctónica (paneles inferiores) y del componente del stress del viento paralelo a la costa en dirección al ecuador en dinas cm^{-2} (paneles superiores), correspondientes a las cuatro áreas de acumulación.

INTERACCION FISICA Y BIOLOGICA INTERANUAL DE GRAN ESCALA EN LA CORRIENTE DE CALIFORNIA

Antes de referirnos a la variabilidad interanual, discutiremos brevemente la variación estacional. La figura 7 muestra los promedios mensuales de biomasa (paneles inferiores) junto al ciclo estacional del componente paralelo a la costa del stress del viento en dirección al ecuador (Nelson 1977). Estos valores del stress del viento pueden ser considerados como un índice de surgencias costeras, con un aumento en su magnitud correspondiendo a un incremento de las surgencias. En los datos de biomasa existe un claro gradiente latitudinal de norte a sur, con valores más elevados en el norte. Por otra parte, como se mostró en la Tabla 1, la estacionalidad en las dos áreas norte es más pronunciada siendo responsable por 30 y 23% de la varianza total respectivamente.

Al inspeccionar la relación entre ambas variables, ocasionalmente se observa una buena correspondencia. Por ejemplo, un máximo del stress del viento durante Mayo en el área III, es seguido de un máximo de biomasa en Junio; y nuevamente un máximo del stress en Septiembre, es seguido un mes más tarde por otro máximo en la biomasa. De aquí podría concluirse que existe una relación estrecha entre ambos procesos. Sin embargo, esta relación no se mantiene para las otras áreas. En todo caso, explorar relaciones causales entre ciclos estacionales es un ejercicio estadísticamente arriesgado por dos razones. En primer lugar el limitado número de grados de libertad (12), con variables generalmente fuertemente autocorrelacionadas, hace que el número efectivo disponible para las comparaciones sea aún menor. En segundo lugar, casi todas las series geofísicas y biológicas presentan estacionalidad, y permitiéndose cierta libertad con los desfasamientos entre variables, es siempre posible encontrar una correlación significativa. Un análisis de correlación entre el stress paralelo a la costa considerado como índice de surgencia y la biomasa de zooplancton, demostró que todos los valores de correlación en las cuatro áreas no son significativos para desfasamientos de 0 a 24 meses, obteniéndose valores menores a 0.25 en todos los casos. Es legítimo concluir entonces que las surgencias costeras no constituyen el proceso dominante que controla la variación interanual de la respuesta biológica en las corrientes de margen oriental.

Una interpretación conservadora de estos resultados, nos permite suponer la existencia de otros procesos que explique en parte la variabilidad biológica observada en las series. En el resto de este trabajo, discutiremos exclusivamente residuales no-estacionales de las variables.

La contraparte física de las series de biomasa en California, series de temperatura, salinidad y transporte, se obtuvieron en base a datos colectados en las estaciones que se muestran en la figura 8. Estas estaciones son aquellas que fueron ocupadas en mayor frecuencia temporal.

Atendiendo a la fuerte co-variación de las series de biomasa, y con el fin de generar una serie única representativa para toda la región, se calculó un promedio entre las series de las cuatro áreas. Este promedio toma en cuenta, por medio de un procedimiento estadístico objetivo, la presencia de vacíos en las series, (detalles del método se entregan en: Chelton, Bernal y McGowan, 1982). Las correlaciones entre esta serie única y las series por área son 0.73, 0.89, 0.89 y 0.73 para las áreas I, II, III y IV respectivamente. Esta serie única se muestra en la figura 9a, junto a series de temperatura (9b), salinidad (9c) y transporte (9d). Las series de temperatura y salinidad representan valores mensuales, promediados sobre toda el área, de las observaciones a 10 m de profundidad. Chelton (1981) demostró que el campo de temperatura es altamente coherente sobre toda la región de la Corriente de California, y que el de salinidad, aunque más ruidoso, tiende a aumentar y disminuir en el mismo sentido sobre toda la región.

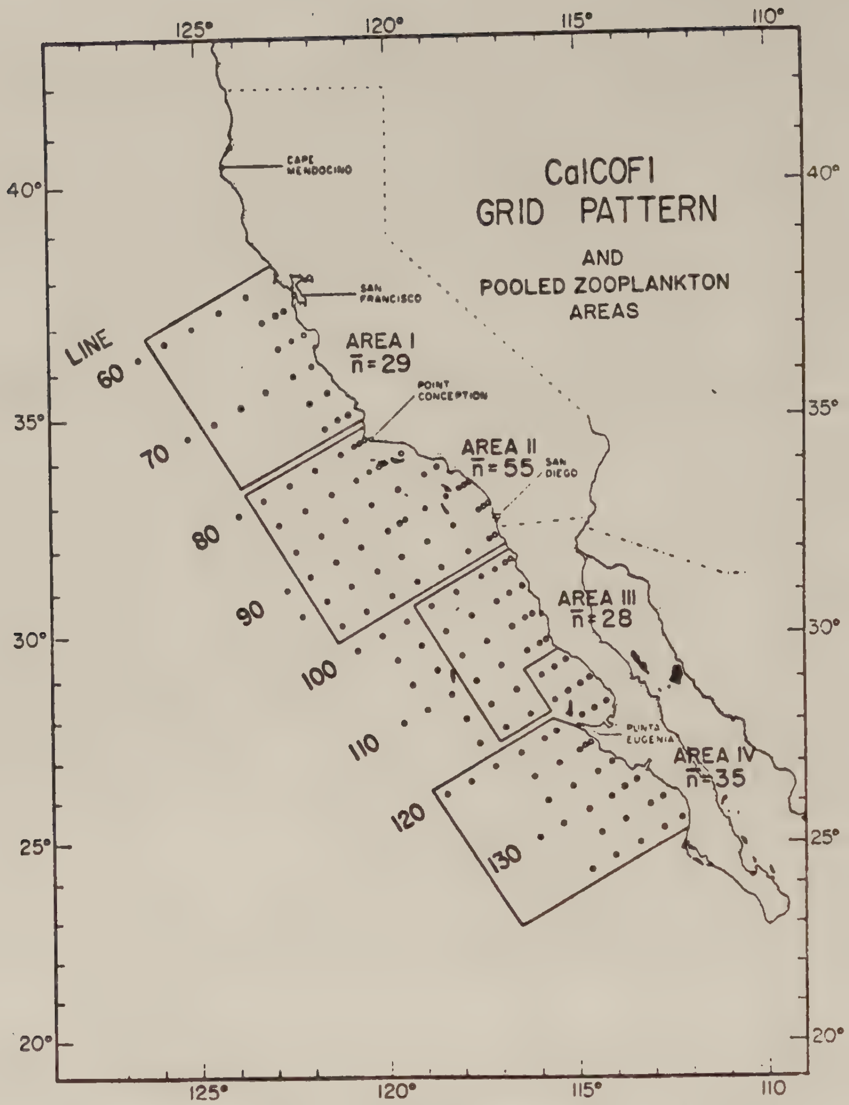

125°
120°
115°
110°
40°
35°
30°
25°
20°
CalCOFI
GRID PATTERN
AND
POOLED ZOOPLANKTON
AREAS
CAPE MENDOCINO
SAN FRANCISCO
AREA I
n̄=29
POINT CONCEPTION
AREA II
n̄=55
SAN DIEGO
AREA III
n̄=28
PUNTA EUGENIA
AREA IV
n̄=35
LINE
60
70
80
90
100
110
120
130
110

Fig. 8.- Red de estaciones hidrográficas frecuentemente ocupadas en el Programa CalCOFI: Los círculos abiertos representan estaciones sobre profundidades de menos de 500 m. Las áreas de acumulación para la biomasa zooplanctónica aparecen como cajas con línea contínua.

La información de transporte, fue tratada en forma diferente. Primero se calculó el campo de alturas dinámicas integradas sobre 500 dB y luego se llevó a cabo una descomposición ortogonal de la matriz de autocovarianza de este campo. Este procedimiento, conocido como Funciones Ortogonales Empíricas (F.O.E.), busca definir patrones espaciales invariantes que den cuenta de una alta proporción de la varianza temporal total del campo observada durante el período en estudio. Cada observavión mensual del campo (un mapa de alturas dinámicas) es descompuesto en un número limitado de componentes, (los patrones espaciales invariantes) ponderados por coeficientes temporales proporcionales a la importancia que cada patrón muestra en el mes en cuestión. La figura 10 muestra el patrón invariante asociado a la primera F.O.E. y en el panel d de la figura 9 se presenta la variación temporal del mismo, considerado como transporte anómalo de gran escala. Superpuesta a la serie de transportes, se ha incluido la serie biológica representada por triángulos. Resulta evidente que la respuesta biológica del sistema está estrechamente asociada a estas variaciones del transporte de la corriente.

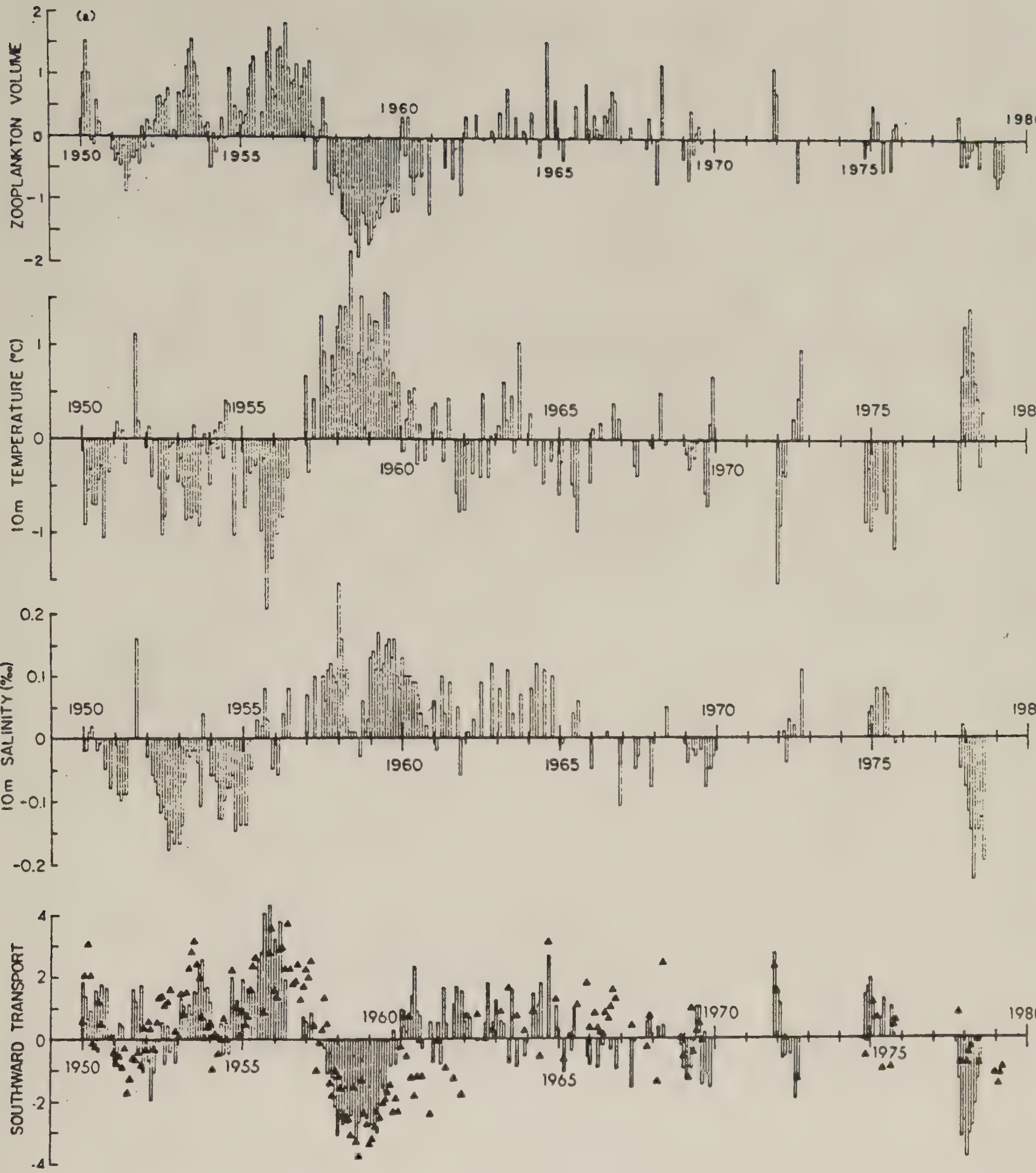


Fig. 9.- Series de tiempo de residuales no estacionales de cuatro parámetros en la Corriente de California: a) Serie única de residuales de biomasa de zoopláncton (promedio de las cuatro áreas); b) temperatura promedio a 10 m sobre 150 estaciones hidrográficas; c) salinidad promedio a 10 m sobre 150 estaciones hidrográficas; d) serie de tiempo de los coeficientes de amplitud de la primera Función Ortogonal Empírica de alturas dinámicas 0/500 decibars, los triángulos representan la serie de biomasa zooplanctónica 9a..

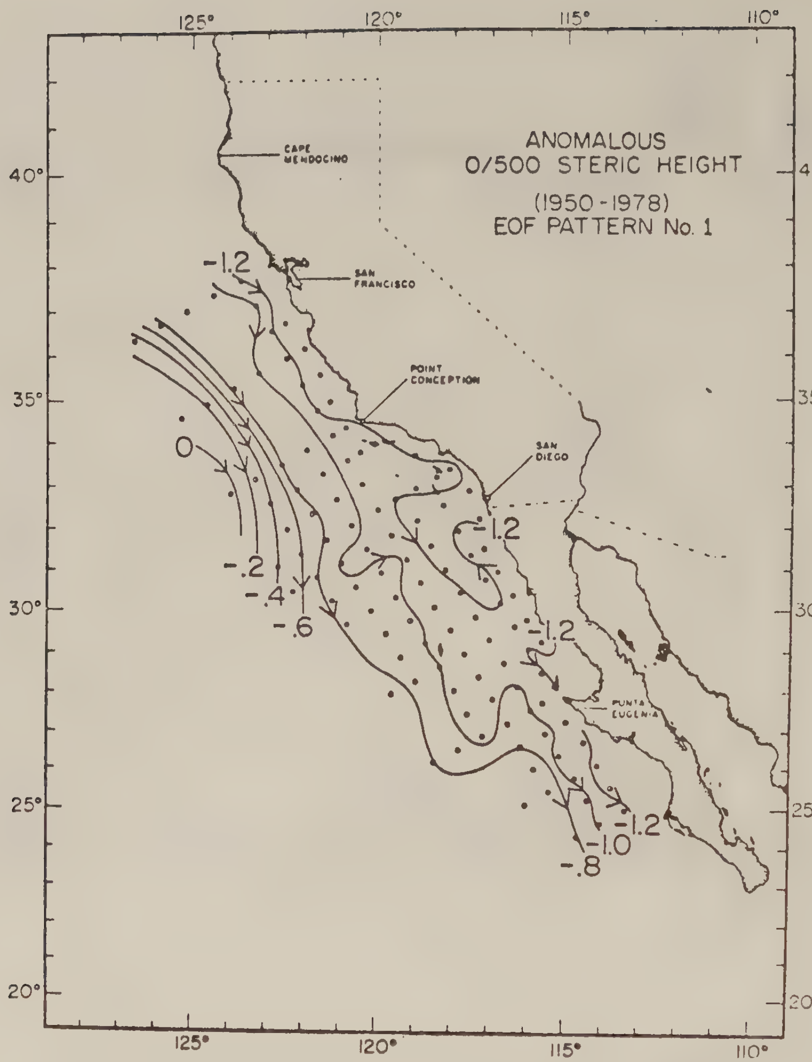

ANOMALOUS
0/500 STERIC HEIGHT
(1950-1978)
EOF PATTERN No. 1
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
-1.2
0
-.2
-.4
-.6
-1.2
-1.2
-1.2
-1.0
-.8
125°
120°
115°
110°
40°
35°
30°
25°
20°

Fig. 10.- Patrón espacial invariante representativo de la primera función Ortogonal Empírica de alturas dinámicas. Las flechas indican la dirección del flujo cuando la serie de tiempo de los coeficientes de amplitud es positiva.

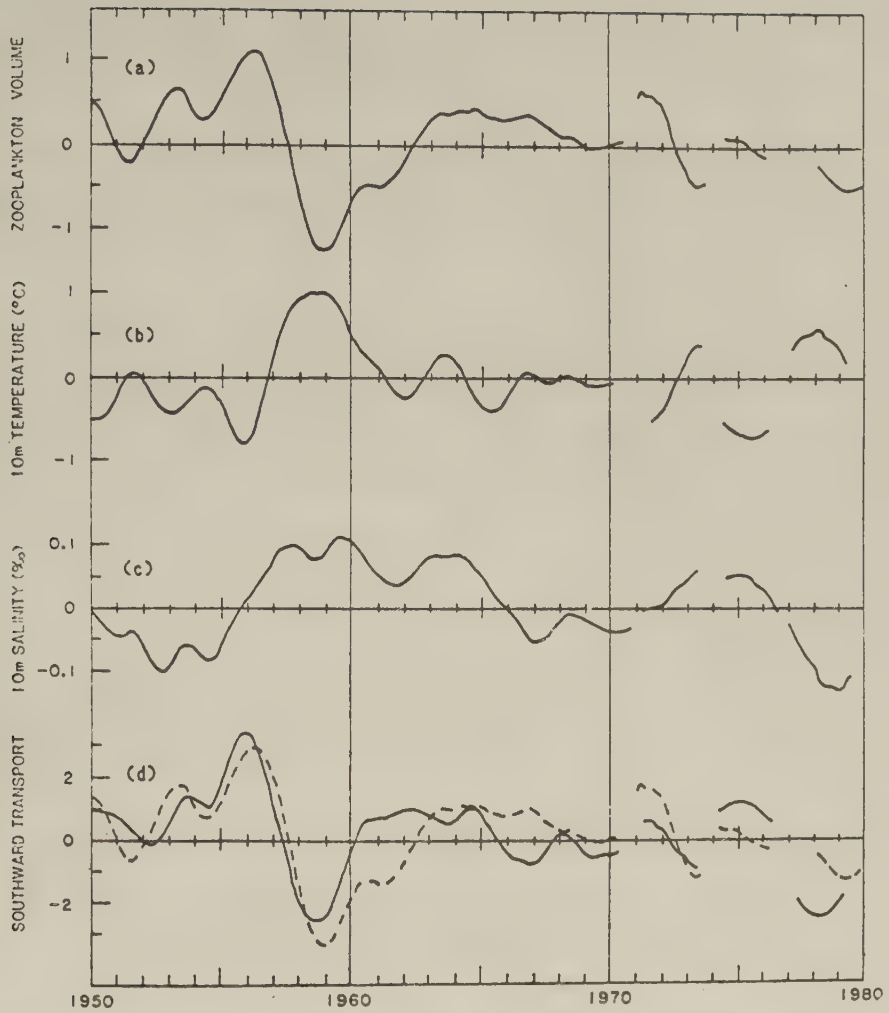


Fig. 11.- Componente de variación interanual de las cuatro series de tiempo de la Figura 9. La línea punteada en 11d, representa la serie de biomasa zooplanctónica.

Una representación más compacta de la variabilidad de estas series, se muestra en la figura 11, donde se ha dejado solamente el componente interanual de la variabilidad al computarse el promedio móvil de 13 meses sobre los datos de la figura anterior. También en este caso se consideró objetivamente, la presencia de vacíos en las series.

De la comparación de estas series, resulta evidente que existe una relación inversa entre zooplancton y la temperatura. La correlación máxima es -0.77, con la temperatura precediendo al zooplancton por 6 meses. Valores por sobre o debajo de 0.33 son significativos con un límite de confianza del 95%. Esta asociación aunque importante en sí misma, no permite separar los dos procesos que pueden establecer un vínculo causal entre ambas series: la advección horizontal y la advección vertical. Ambos procesos físicos están estrechamente ligados, ya que un aumento en el flujo de la Corriente de California resulta en un incremento de la advección de aguas frías de origen subártico, pero también provoca un ajuste geostrófico del campo de densidad que resulta en un levantamiento de las isotermas y enfría la zona costera mediante advección vertical.

Estos procesos podrían ser distinguidos mediante las variaciones del campo de salinidad, ya que la distribución zonal y meridional de esta variable en la Corriente de California, hace que la advección horizontal disminuya la salinidad superficial y que la advección vertical la aumente. Como se mencionó, el campo de salinidad es más ruidoso y más heterogéneo en el espacio que el de temperatura. La variación interanual de la salinidad es muy pequeña (desviación estándar de 0.06 o/oo) y la relación entre temperatura y salinidad que resulta es débil. La máxima correlación observada es de 0.36, valor que es significativo sólo con un intervalo de confianza del 75%. De estos dos análisis es posible concluir que tanto la advección horizontal como la vertical juegan un rol en el control de las fluctuaciones interanuales del zooplancton. Debe recalcarse que la advección vertical a la que nos referimos, no se trata de surgencias costeras inducidas localmente por el viento, sino que es producto del reajuste geostrófico del campo de densidad, es decir, por un cambio en la inclinación de las isopicnas en respuesta a cambios de gran escala y baja frecuencia en el transporte de la Corriente de California.

Son precisamente las fluctuaciones dominantes del flujo de gran escala las que estan siendo medidas por la primera función ortogonal empírica en la figura 11d. Esta figura presta un apoyo contundente a la hipótesis que el aumento del transporte hacia el ecuador está asociado con un aumento de la biomasa zooplanctónica y que una disminución de este transporte produce el efecto inverso.

La función de correlación desfasada entre estas series es claramente asimétrica indicando que el zooplancton está mas fuertemente correlacionado con el flujo anómalo cuando este lo precede. Se observa una correlación máxima de 0.77 cuando las variaciones del transporte preceden al zooplancton por 5 meses. Para esta comparación, valores a 0.35 son significativos con un límite de confianza del 95%. Este es un resultado extraordinariamente bueno si se consideran los serios problemas del muestreo presentes en la base de datos originales

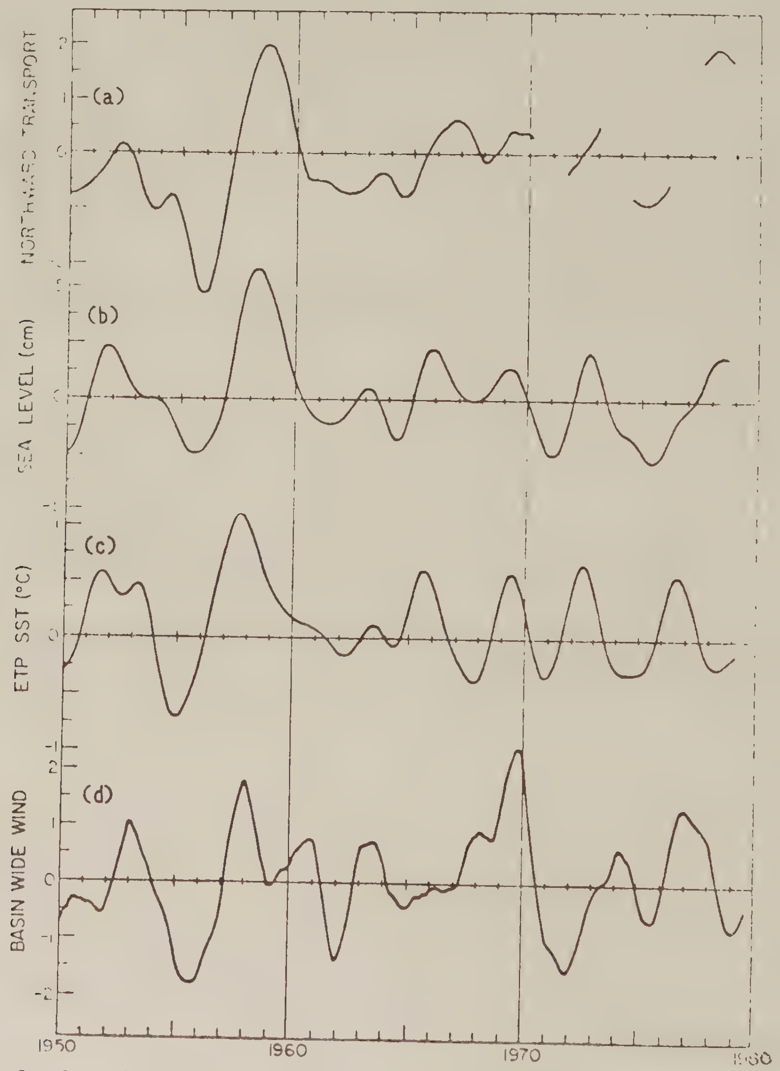


Fig. 12.- Series de tiempo de la variación de baja frecuencia, calculada por la doble aplicación de promedios móviles de 13 meses. a) índice de transporte hacia el norte; b) el nivel del mar promedio para California calculado en base a datos de San Francisco, Los Angeles y San Diego; c) anomalías de la temperatura superficial del mar en el Pacífico Ecuatorial Oriental indicativas de El Niño; d) Serie de los coeficientes de amplitud del patrón invariante dominante de los vientos sobre el Pacífico norte (Fig. 13).

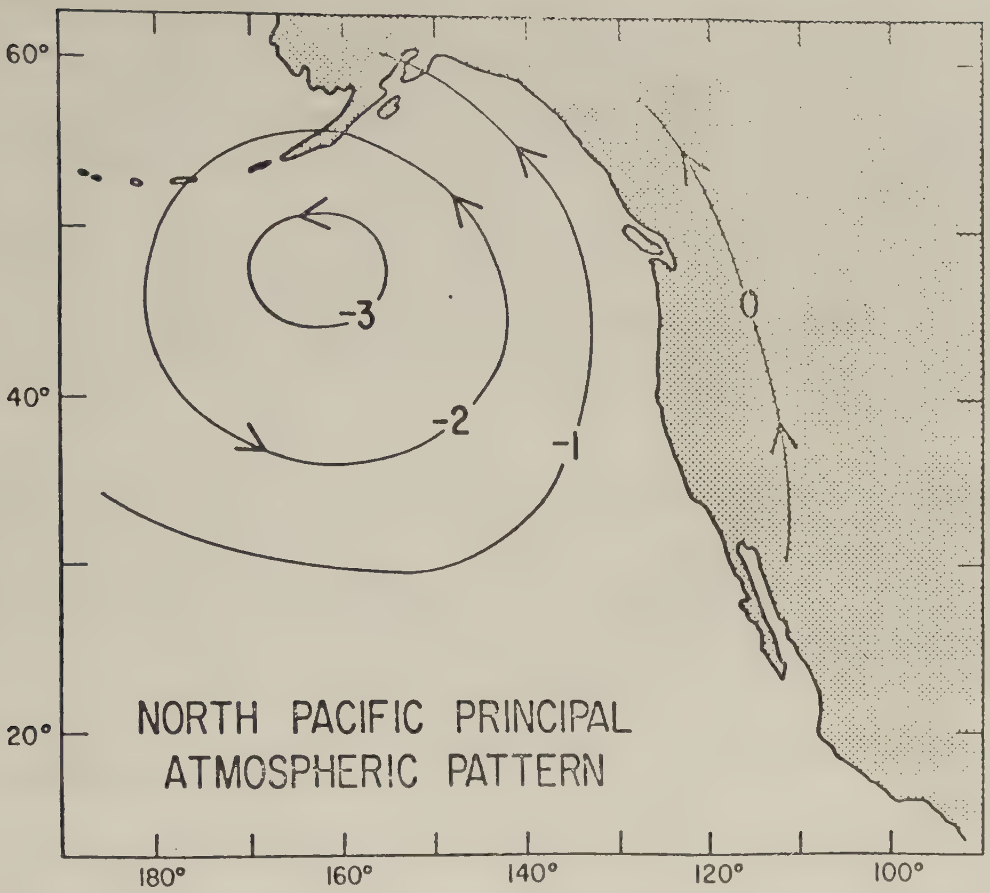


Fig. 13.- El patrón principal de variación de los vientos sobre el Pacífico Norte. Las flechas indican la dirección del flujo geostrófico cuando las amplitudes se consideran como positivas, (de: Davis, 1978).

Con el propósito de buscar un método que permita monitorear estas fluctuaciones de gran escala, se exploró la relación entre el flujo anómalo de la corriente con las alturas del nivel del mar registradas en mareógrafos costeros. La figura 12b presenta series de nivel del mar suavizadas con un doble promedio móvil de 13 meses para San Francisco, Los Angeles y San Diego. Los valores han sido corregidos respecto a los efectos barométricos inversos de la presión atmosférica. La figura 12a muestra las variaciones de flujo anómalo hacia el norte (la misma serie referida al patrón invariante con signo cambiado). Es aparente que existe una estrecha relación entre el flujo de la Corriente de California y el nivel del mar en la costa. Niveles del mar elevados se corresponden con flujo anómalo en dirección al norte y bajos niveles del mar indican flujos hacia el ecuador mayores que el promedio. La correlación máxima entre estas series es de 0.83, con valores mayores a 0.30 significativos al 95%. Esta máxima asociación se observa cuando la elevación costera del nivel del mar precede al transporte por 3 meses. Obviamente, de acuerdo a los resultados previos, las series de nivel del mar medido en la costa están también estrechamente asociadas a la variabilidad de gran escala del zooplancton, con una correlación máxima de -0.70 cuando el nivel del mar precede al zooplancton por 7 meses (significativo al 95%).

La causa de las variaciones de gran escala en el flujo de la corriente de California no está claramente establecida. Sin embargo, se observa una estrecha asociación entre estas fluctuaciones y los fenómenos de El Niño. En la figura 12c se muestran las anomalías térmicas en el Pacífico Ecuatorial Oriental (0°-10°S; 80°-100°W). La correlación máxima entre ambas series es de 0.74, con valores mayores a 0.39 significativos al 95% cuando anomalías positivas en el Pacífico Ecuatorial Oriental preceden las anomalías del flujo en California por 3-4 meses. Chelton y Davis (1982) demostraron que el intervalo de tiempo por el cual las variaciones térmicas del Pacífico Ecuatorial Oriental, preceden los cambios de nivel del mar a lo largo de la costa occidental de Norteamérica, aumentan monotónicamente a mayor distancia de los trópicos. Esta relación permite derivar una velocidad de propagación de fase para la perturbación de 40 cm, seg^{-1}. Esta observación es consistente con modelos de El Niño que proponen que esta perturbación se propage en la forma de ondas costeras atrapadas o de Kelvin (McCreary, 1976), aunque la velocidad de propagación es sólo un tercio de lo esperado. En dicho estudio también se observó que la zona de flujo geostrófico oceánico asociado, es mucho más ancha que la predicción del modelo, lo que permite sugerir la presencia de ondas de Rossby propagándose hacia el oeste. Esta relación entre las anomalías térmicas del Pacífico Ecuatorial Oriental y el flujo anómalo de la Corriente de California, sin embargo, no da cuenta de algunos períodos anómalos, por ejemplo 1953, 1967-68, 1976 y 1978.

En la figura 12d se muestra la serie de tiempo de la variación de gran escala de los vientos sobre el Pacífico Norte. Estas son estimaciones cuasi-geostróficas de los vientos, a escala de toda la cuenca. El patrón espacial dominante de los vientos se muestra en la figura 13, donde los valores negativos indican circulación anticiclónica. Sorprendentemente se observa una correlación máxima de 0.43, cuando el nivel del mar precede a los vientos por tres meses.

Esta inesperada relación puede comenzar a entenderse al considerar la correlación entre las anomalías térmicas del Pacífico Tropical Oriental en relación a los vientos. En este caso la temperatura en el Pacífico Ecuatorial Oriental precede a los vientos por seis meses, mostrando una correlación de 0.48. Esta relación pone de relive la importancia de las teleconecciones que se dan en la atmósfera entre procesos que tienen lugar en la banda ecuatorial y en latitudes intermedias, es decir, los procesos transientes que ocurren en la atmósfera por la alternancia del dominio de las circulaciones de Walker y Hadley y que parecieran tener un rol dominante en la génesis de perturbaciones de El Niño.

- REFERENCIAS

Bernal, P.A. 1979. Large-scale biological events in the California Current. Calif.Coop.Oceanic Fish.Inv.Rep. (20):89-101.

Bernal, P.A. 1980. Large-scale biological events in the California Current: the biological response of the epipelagic ecosystem. Ph.D. Dissertation, Scripps Institution Oceanography, University of California of San Diego. 184 pp.

Bernal, P.A. y J.A. McGowan. 1981. Advection and upwelling in the California Current. pp. 381-399. In Coastal upwelling (F. Richards, ed.). A.G.U. Washington, D.C.

Chelton, D.B. 1981. Interannual variability of the California current physical factors. Calif.Coop. Oceanic Fish.Inv.Rept. (22):34-48.

Chelton, D.B. y R.E. Davis. 1982. Monthly mean sea level variability along the west coast of North America. J.Phys.Oceanog. (12):757-784.

Chelton, D.B., P.A. Bernal y J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J.Mar.Res. 40:1095-1125.

Colebrook, J.M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955-59. Fish.Bull.US. 75:357-368.

Haury, L.R. 1976. A comparison of zooplankton patterns in the California Current and the North Pacific central gyre. Mar.Biol. 28:37-49.

Hayward, T.L. y J.A. McGowan. 1979. Pattern and structure in an oceanic zooplankton community. Amer.Zool. 19:1045-1055.

McCreary, J.P. 1976. Eastern tropical response to changing wind systems: with application to El Niño. J.Phys.Oceanog. 6:632-645.

McGowan, J.A. 1974. The nature of oceanic ecosystems. pp. 9-28. In The biology of the oceanic Pacific (C.B. Miller, ed.). Oregon State University Press, Corvallis.

Nelson, C.S. 1977. Wind stress and wind stress curl over the California Current. NOAA Tech.Rep. NMFS-SSRF-714, August 1977.

Reid, J.L. 1962. On the circulation, phosphate-phosphorous content and zooplankton volumes in the upper part of the Pacific Ocean. Limnol.Oceanog. 7:287-306.

Ryther, J.H., D.W. Menzel, E.M. Hulburt, C.J. Lorenzen y N. Corwin. 1971. The production and utilization of organic matter in the Peru Coastal Current. Inv.Pesq. 35:43-60.

Soutar, A. y J.D. Isaacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. Calif.Coop.Oceanic.Fish.Inv.Rept. 13:63-70.

____________. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off the Californias. Fish.Bull.US. 72:257-273.

Venrick, E.L., J.A. McGowan y A.W. Mantyla. 1973. Deep chlorophyll maxima in the oceanic Pacific. Fish.Bull.US. 71:41-52.

Walsh, J.J. 1977. A biological sketchbook of an eastern boundary current. pp. 923-968. In The sea, Vol. 6 (E.D. Goldberg, I.N. McCave, J.J. O'Brien and J.H. Steele, eds). Interscience, New York.

Wickett, W.P. 1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J.Fish.Res.Bd.Canada. 24:581-594

OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

COMPARATIVE CLIMATOLOGY OF SELECTED ENVIRONMENTAL PROCESSES IN RELATION TO EASTERN BOUNDARY CURRENT PELAGIC FISH REPRODUCTION

by

Richard H. Parrish, Andrew Bakun, David M. Husby and Craig S. Nelson

Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831
Monterey, California 93942
USA

Resumen

Las principales regiones oceánicas del mundo con corrientes marinas en sus confines orientales (i.e., Sistemas de California, Perú, Canarias y Benguela) parecen comportar dinámicas ambientales similares y contienen congregaciones similares de especies de peces pelágicos. En la medida en que especies correspondientes a diferentes sistemas funcionen como análogos, los estudios comparativos interregionales pueden producir información relativa a los efectos del ambiente en el éxito de la reproducción. Lo que de otra forma sería difícil de obtener de un sólo sistema regional.

Los archivos históricos con informes del clima marino proporcionan una fuente de datos en formatos similares sobre la climatología de procesos oceánicos en varias regiones. Estos forman la base para reconocer las diferencias y semejanzas en las diversas áreas de desove de especies correspondientes. La selección natural implica que los hábitos reproductivos en cada caso representan la adaptación a los factores ambientales más cruciales. Por lo tanto los patrones de las relaciones de la reproducción y el ambiente sugieren la existencia de enlances de causalidad importantes.

Esta forma de deducir los factores ambientales que son cruciales puede dar una base racional para limitar las alternativas en cuanto a las variables que pueden explicar estos procesos. Permitiendo de esta forma el uso más efectivo de las series de datos en la formulación de modelos donde el reclutamiento es dependiente de las condiciones ambientales. Además, el concentrarse en los principales interacciones stock - ambiente puede proveer las bases para utilizar la experiencia que se gana en un sistema para predecir el resultado de acciones en otro sistema.

Normalmente los datos sobre las variables causales primarias (alimento, predación, mortalidad dependiente de la densidad, etc) no están disponibles. Por lo tanto nos concentramos en varios procesos que pueden ser abordados usando datos del mar. Se piensa que estos procesos pueden tener un impacto en los estadios tempranos de la vida de los peces al alterar las variables causales primarias, particularmente el alimento. Estos incluyen: (1) mezcla por turbulencia generada por el viento, que puede dispersar las concentraciones de pequeña escala de las partículas de alimento necesarios para que las larvas se alimenten por primera vez en forma éxitosa; (2) transporte mar afuera, que puede arrastrar los huevos y larvas planctónicos fuera de las áreas costeras que le son favorables; (3) afloramientos costeros, que pueden ser favorables si se presentan con un retraso apropiado pero son perjudiciales si coinciden en espacio y tiempo con el desove. La temperatura es una variable causativa primaria por sus efectos directos sobre procesos fisiológicos.

Los cuatro principales sistemas de corrientes de los confines orientales del mar tienen mucho en común. La ubicación y estacionalidad del máximo transporte Ekman mar afuera parece estar estrechamente relacionado con el desplazamiento latitudinal y estacional de los sistemas de presión atmósferica y con las relaciones entre estos sistemas y la topografía de los continentes. Sin embargo, como se puede ver de las características ambientales que se presentan, hay también grandes diferencias entre ellas. Por ejemplo, los cuatro sistemas tienen anomalías máximas de bajas temperaturas mar afuera mar adento, asociadas con el máximo transporte mar afuera de Ekman de varano. En estas regiones de máximos afloramientos de verano se encuentran stocks de anchoveta y/o sardina con áreas de desove desplazadas hacia el polo y hacia el ecuador. Los sistemas de California y de Benguela tienen, ambos, una sóla área con anomalías superficiales de baja temperatura. En el sistema de California esta área está ubicada en el área de máximo afloramiento de verano, mientras que el sistema de Benguela tiene un área de afloramiento máxima de verano en Luderitz y un área de afloramiento máximo de invierno en Cabo Frío. Los sistemas de Perú y las Canarias tienen cada uno dos áreas separadas de anomalías superficiales de baja temperatura. El sistema peruano tiene un área localizada en el área de máximo afloramiento de invierno (San Juan o Chimbote) y una segunda área en la zona de afloramiento frente a la parte central de Chile, que tiene un máximo de verano en Talcahuano. El sistema de Canarias tiene un afloramiento máximo de verano frente a Lisboa y un segundo afloramiento máximo de verano entre Cabo Sim y Cabo Blanc. Durante el invierno la anomalía de aguas frias frente al noroeste de Africa se desplaza al sur y el máximo del afloramiento se extiende de Cabo Blanc a Cabo Vert.

Los centros de afloramiento (caracterizados por un fuerte transporte mar afuera, intensa mezcla por turbulencia generada por el viento, y reducida estabilidad de la columna de agua) parecen ser evitados como parte de los hábitos de desove. Las áreas de desove de anchovetas y sardinas tienden a estar en las áreas costeras donde el transporte y turbulencia inducidos por el viento son reducidos y la plataforma continental tiende a ser más amplia. Las áreas de desove de las poblaciones más grandes tienden a estar corriente abajo (hacia el ecuador) con respecto a los centros de afloramiento. La población de anchoveta (que ha sido el más grande de todos los stocks actuales de sistemas de corrientes de los confines orientales del mar) desova en un área de fuerte afloramiento. Nuestra hipótesis es que en este caso el ambiente costero particularmente amplio, y la dependencia de la profundidad de la capa de Ekman de la latitud y la estratificación puede servir para reducir el efecto perjudicial del transporte superficial mar afuera de Ekman.

Los patrones para evitar la mezcla por turbulencia y el transporte mar afuera en los hábitos reproductivos sugieren que estos procesos han ejercido un importante control sobre el éxito de la reproducción. Aparentemente estas variables merecen ser consideradas al modelar las variaciones del reclutamiento. En regiones donde las temperaturas características se encuentran dentro de límites fisiológicos, la temperatura no parece ser un factor dominante al determinar el ambiente para el desove.

La capa mínima de oxígeno frente al Perú es muy superficial en comparación con otras regiones. Se sugiere que esto puede conducir a menor competencia entre los stocks de peces pelágicos y los mesopelágicos.

INTRODUCTION

In this work we have developed climatological fields of oceanographic and meterological data for the four "classical" eastern boundary current systems (Wooster and Reid, 1963). We attempt, through pattern recognition, to define similarities and differences in the characteristic environmental conditions in the spawning grounds of the recognized stocks of pilchard (Sardina and Sardinops) and anchovy (Engraulis) in these systems. Our approach is similar to Reid's (1967) analysis of the oceanic environs of the genus Engraulis. He included the entire life`cycle and described the range of surface temperature and salinity in which Engraulis occurs. We have limited our comparisons to the environments in which the early life history stages occur (i.e., the spawning grounds) and have expanded the list of environmental variables.

A major motivation for international cooperation in fisheries research is the assumption that research methods and/or results derived from studying one population can be transferred to another. For example, the recently proposed "International Recruitment Experiment" (IREX)[2] is based on the hypothesis that the biological responses to environmental conditions are similar for separate stocks of closely related species. The IREX proposal identifies six variables which are thought to account for most of the biological variability observed in exploited fishes. These variables are temperature, turbulence, transport, food, predation, and population density. Population variations of stocks within a species group, or even in an individual stock, could be caused by any, or all, of the six variables. The hypothesis does not imply that different stocks of a given species group have the same environmental variable as their limiting factor. Rather it implies that the stocks have a similiar functional relationship to that environmental variable.

In this work we are addressing a narrow subset within the IREX construct. The species groups considered are anchovies and pilchards, and we are limiting the analyses to comparisons of the environments of their spawning grounds in the four major eastern boundary currents. The regions of interest consist of the California Current off western North America, the Peru Current off western South America, the Canary Current off the Iberian Peninsula and northwestern Africa, and the Benguela Current off southwestern Africa (Fig. 1). Data which could be used to compare the predation, food, and density variables are not available for the spawning grounds of most of the stocks in the California, Peru, Canary, and Benguela Currents. We are therefore basing our comparisons upon several processes which can be indicated by available maritime data. These processes are thought to have important impacts on the early life history of the two species groups by altering the primary causative variables, particularly food. From the point of view of the utility of the study, results based on routinely available data offer the possibility of being followed in real time for management purposes.

Eastern boundary currents are characterized by equatorward surface flow and coastal upwelling. One result of these factors is that the eastern sides of the oceans have a very extensive temperate zone. For example, the 20° and 10°C isotherms at 10 meters occur at lat. 27°N and 60°N in the eastern North Pacific, and in comparison they occur at lat. 40°N and 45°N in the western North Pacific (Barkley, 1968). Another feature of eastern boundary current regions is the tendency for narrow continental shelves. Consequently the fisheries of eastern boundary currents are dominated by a small number of temperate pelagic fishes which can achieve very large populations. The physical environments of the four major eastern boundary currents are quite similar and therefore it is not surprising that their fisheries are dominated by very closely related, geographically isolated stocks or species (Table 1). Pilchards, anchovies, jack mackerel (Trachurus), and hake (Merluccius) achieve the largest populations; mackerel (Scomber japonicus) and bonito (Sarda) also are important in the fisheries of the eastern boundary currents, although they don't attain the population size of the other four species groups.

---

[2] Report of Scientific Committee on Ocean Research (SCOR) and Advisory Committee of Experts on Marine Resources Research (ACMRR), Working Group 67 (Oceanography, Marine Ecology and Living Resources) developed in response to the Ocean Sciences in Relation to Living Resources (OSLR) resolution of the Intergovernmental Oceanographic Commission (IOC), 1 July 1982.

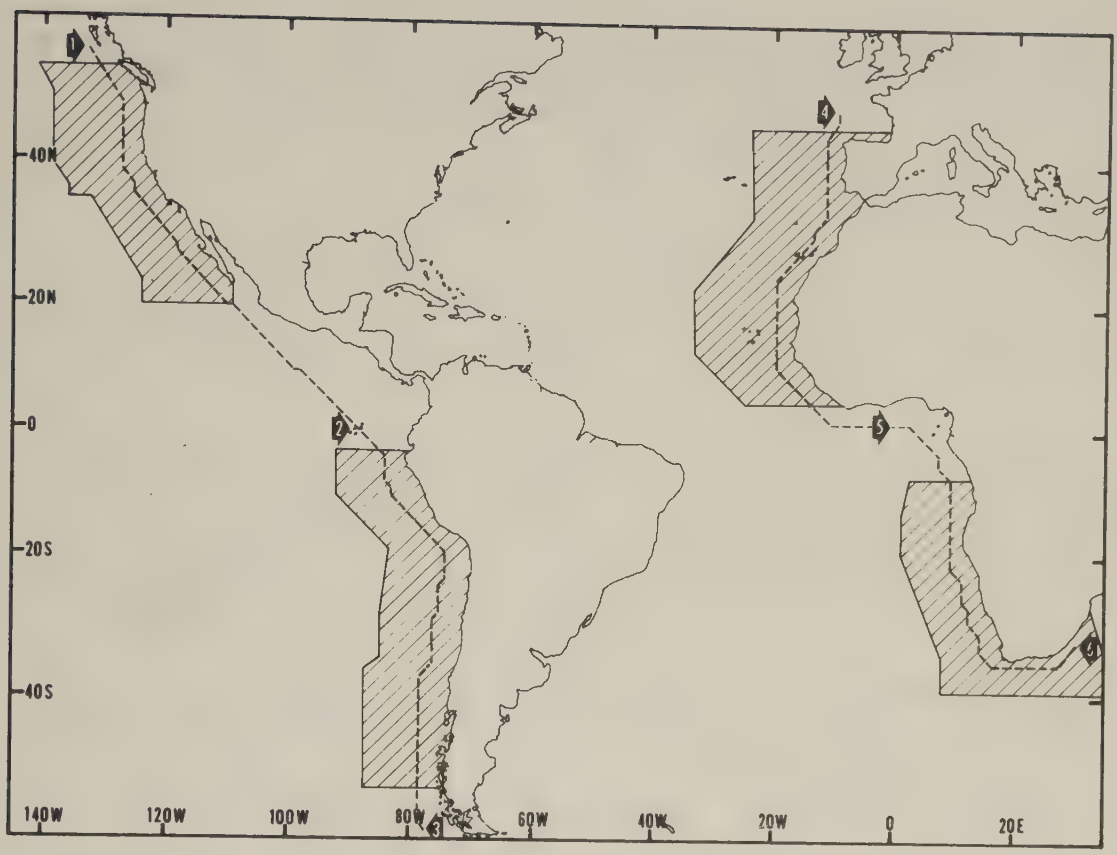


Figure 1. Geographical orientation of various summaries presented in this paper. Appendix maps are assembled from summaries within 1-degree areal segments of the four eastern boundary current regions indicated by diagonal hatching. Alongshore vertical sections (Figs. 3-6) are arranged along the dashed lines near the eastern ocean boundaries.

TABLE 1. Dominant anchovy, pilchard, horse mackerel, hake, mackerel, and bonito in the four major eastern boundary currents (after Bakun and Parrish, 1980).

CALIFORNIA CURRENT	PERU CURRENT	CANARY CURRENT	BENGUELA CURRENT
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardina pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Merluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

Fisheries for pilchards and anchovies are notorious for their extreme variability. All four current systems at one time or another have had fisheries dominated by pilchards (Fig. 2). The northern stock in the California Current system (Radovich, 1981) and the Namibian (Troadec, Clark, and Gulland, 1980) and South African (Cram, 1981) stocks in the Benguela Current system have collapsed under heavy exploitation. The Peru Current system (Serra et al., 1979) and the Canary Current system (FAO, 1978) have had recent increases in the size of pilchard stocks, and landings in these regions are presently dominated by pilchards. Conversely, anchovies presently dominate the landings in the Benguela and California Current systems and appear to be abundant, although lightly exploited in the Canary Current system. The collapse of the Peru anchoveta stock under heavy exploitation is well known (Tomczak, 1981).

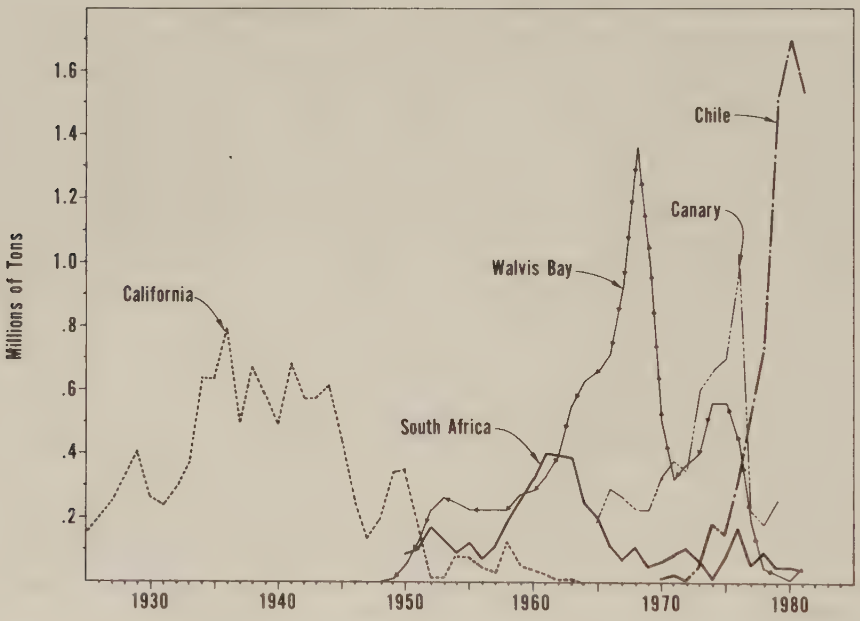


Figure 2. Yearly pilchard (sardine) landings from several eastern boundary current stocks.

The basis for our comparison is, like the IREX proposal, dependent upon the hypothesis that closely related stocks or species have similar early life history requirements. This would suggest that the environments of the various spawning grounds are similar. That is, in the mean they should fall within the tolerance range of the species group. This does not imply that environmental conditions in the spawning grounds are optimal, only that stocks have recently maintained populations by spawning there.

How unrelated may the stocks be before this hypothesis becomes ridiculous? Most fisheries biologists would probably agree[3/] that the present California stock of pilchard (sardine) has the same physiological requirements as the stock had in the 1930's before it collapsed. However, the present remnant of the stock may have a different gene pool than the original. Most fisheries biologists would probably agree[3/] that, within a given species, physiology is nearly identical. Taxonomic distinctions at the species-generic level are quite plastic. The mackerel stocks of the eastern boundary currents are now considered to belong to the same species, Scomber japonicus. Just a few years ago they were considered to be different species and the genus was not Scomber but Pneumatophorus. Each eastern boundary current presently has a different species of Engraulis. These "species" are very similar and it takes considerable expertise to tell them apart. To quote McDowell (1962), "There are grounds for suspicion that this expertise is not possessed by the fish themselves...." We are assuming that in the case of geographically separated stocks of closely related species the differences in the physiological requirements of the early life history stages are negligible.

To provide a basis for our comparisons, historical subsurface oceanographic data and surface marine weather observations are used to examine the large-scale spatial and seasonal patterns of several environmental parameters which appear to have had important effects on the spawning habits of pelagic fishes in eastern boundary current systems. Our comparative studies are primarily focused on the atmosphere-ocean processes related to horizontal and vertical advection, vertical stability, and temperature. Bakun and Parrish (1980) discussed the rationale for selecting the particular suite of oceanic and atmospheric properties described in this study.

Characteristic annual mean distributions of oceanographic data and summer and winter climatologies based on surface marine weather observations are presented in the Appendix as charts of surface geostrophic flow, sea surface temperature and coastal temperature anomaly, surface wind-driven transport, an index of wind-generated turbulent mixing, and total cloud amount. The methods used to compile the climatological data are summarized in the Appendix. The format of placing the charts in an appendix, rather than in the text, was selected to facilitate simultaneous intra- and interregional geographic and seasonal comparisons of the large-scale oceanographic and atmospheric properties.

[3/] A hedge word is always necessary when discussing what fisheries biologists will agree upon.

REGIONAL ASPECTS

The surface flow field in eastern boundary current systems, at least on the time and space scales affecting reproductive success of fish stocks (Parrish, Nelson, and Bakun, 1981) can be considered to be a combination of the surface Ekman drift (i.e., the transport of surface waters under the direct action of the wind) and the underlying geostrophic flow field. Highly smoothed representations of the geostrophic flow patterns in the four regional systems (Appendix Chart 1) show major common features. Near the coast, large-scale flow is generally equatorward. At high latitudes the tendency is poleward. Within several hundred kilometers of the coast, a component of large-scale geostrophic flow toward the coast is a common feature. The far offshore regions are characterized by flow toward the coast in the higher-latitude west wind drifts, weak equatorward flow at mid-latitudes, and flow toward the ocean interiors in tropical regions.

Coastal temperature anomaly patterns (Appendix Charts 5 and 6) indicate a general tendency for cool coastal temperatures relative to those offshore. These patterns show local centers of intense cooling associated with coastal upwelling. There also are relatively warm areas within coastal indentations (responding to seasonal warming) and at the high latitude extremes of the regions (associated with warm advection in the poleward flows).

Surface Ekman transport (Appendix Charts 7 and 8) is generally offshore, but becomes onshore at higher latitudes during the winter seasons. Wooster and Reid (1963) have demonstrated that the major geographical and seasonal features of eastern boundary coastal cooling can be related to corresponding features in offshore Ekman transport. Major capes, marking substantial changes in large-scale coastline trend, tend to be regions of maximum offshore Ekman transport and of associated upwelling and coastal cooling.

GEOSTROPHIC CURRENT CHARACTERISTICS

The common large-scale features of the eastern boundary currents have been described by Wooster and Reid (1963). The surface flow in these large systems is predominantly in the sense of the prevailing winds, which is anticyclonic about the mid-ocean atmospheric high pressure cells. The weak (typically less than 50 cm sec^{-1}) equatorward geostrophic flow in eastern boundary currents is due to the baroclinicity of a relatively shallow layer, generally confined to the upper 500 m (Wooster and Reid, 1963).

Another common feature of eastern boundary currents is a poleward flowing undercurrent, which is a subsurface current usually centered at 200-300 m near the continental shelf edge. The waters transported poleward by the undercurrents appear to be enhanced by coastal upwelling and may contribute water to the upwelling centers (Smith, 1978). A poleward countercurrent may occur seasonally at the surface during the winter and during periods when the equatorward wind stress weakens.

Coastal countercurrents are often part of semi-permanent eddy circulations, for example, the Southern California Eddy (Sverdrup and Fleming, 1941). A permanent cyclonic circulation over the continental slope and shelf between Cape Frio and south of Lüderitz in southwest Africa has been postulated by Nelson and Hutchings (MS). In the Canary Current region a cyclonic circulation has been observed in the shallow Banc d'Arguin region south of Cap Blanc (Mittelstaedt, 1974) and may be seen in the schematic diagrams of Rebert (1978).

In addition to the narrow coastal currents and the poleward undercurrents, the large-scale surface circulation in eastern boundary current systems is complicated by the effects of bottom topography and coastline orientation. The advent of satellite infrared imagery of the sea surface and intensive hydrographic surveys in the upwelling regions have identified the existence of many eddy-like features or intense frontal zones associated with upwelling sites or downstream of capes and headlands (Bernstein, Breaker, and Whritner, 1977).

California Current System

The major features of the California Current system have been described by Reid, Roden, and Wyllie (1958), Pavlova (1966), and Hickey (1979). The cool, low salinity waters of the west wind drift diverge at about lat. 45°N, one branch flowing north to feed the Alaskan Current and the other branch flowing southeastward to become the California Current. The equatorward flow between lat. 45°N and 20° N and within about 500 km of the west coast encompasses the bulk of the California Current. Maximum equatorward flow occurs approximately 200-400 km from the coast and is strongest in the summer and early fall. A portion of the California Current turns into the coast at about lat. 30°N and is associated with negative wind stress curl in this region (Nelson, 1977). There is a relatively permanent northward flow near the coast between lat. 30°N and Point Conception (lat. 35°N) which forms the eastern portion of the Southern California Eddy in the Southern California Bight.

The California Undercurrent is a poleward flow of warm, relatively high salinity water at depths of approximately 250-300 m which lies close to the continental slope (Wooster and Jones, 1970). This current is present along the coast from southern Baja California to Vancouver Island (Reed and Halpern, 1976). The northward flow at the surface occuring during the fall and winter along the coast north of Point Conception is commonly called the Davidson Current.

Peru Current System

The north-northwestward flow north of lat. 40°S has been labelled the Peru or Humboldt Current. Gunther (1936) first recognized two branches of this current: a Peru Coastal Current and a Peru Oceanic Current. The northward flow generally splits into the Coastal and Oceanic Currents at about lat. 25°S (Wyrtki, 1965). The annual mean geostrophic flow (Appendix Chart 1) shows this bifurcation at lat. 25°S, long. 76°W and a component of the flow is directed onshore. Both the coastal and oceanic portions of the Peru Current originate in the sub-Antarctic region and transport cold, relatively low salinity water equatorward.

The Peru Countercurrent flows southward at about long. 80°W between the Peru Coastal Current and the Peru Oceanic Current. It is primarily a subsurface current with the strongest flow near 100 m.

The Peru Coastal Current coincides approximately with the upwelling region off Peru and Chile. Coastal bathymetry appears to have considerable influence on the current. Eddies are found wherever the coastal current is deflected strongly from the coast, especially near lat. 15°S (Cañon, 1978). The annual mean surface geostrophic flow is directed onshore north of lat. 15°S and flows strongly onshore in the coastal region between lat. 10°S and 12°S. Wooster and Sievers (1970) noted that the surface drift currents at the coast showed a minimum in equatorward flow between lat. 12°S and 14°S in all seasons, except summer.

During the austral winter the southeast trade winds reach maximum intensity. From April to September the Peru Current appears stronger than in other months and the countercurrent virtually disappears. At this time the two branches of the Peru Current coalesce and the contribution to the South Equatorial Current is the strongest.

The Peru-Chile Undercurrent is a narrow southward flowing countercurrent beneath the Peru Coastal Current. It is found offshore north of lat. 15°S, but south of lat. 15°S it follows close to the coast and can be identified as far as lat. 48°S (Silva and Neshyba, 1979). It is characterized by a low oxygen content.

Canary Current System

The large-scale geostrophic flow in the Canary Current region shows an equatorward component between about lat. 36°N and 20°N. The Canary Current leaves the coast in the vicinity of Cap Blanc (lat. 21°N), which is also the location of persistent upwelling. Cap Blanc is the site of a semi-permanent frontal zone between the North Atlantic Central Water advected southwest by the Canary Current and a low salinity South Atlantic Central Water mass which flows northward along the coast (Hughes and Barton, 1974).

During periods of weak northerly winds, which occur particularly in summer and autumn between lat. 10°N and 20°N, a coastal northwest-flowing countercurrent may be observed (Mittelstaedt, 1974). This coastal countercurrent gives rise to a cyclonic circulation over the shallow Banc d'Arguin south of Cap Blanc. The coastal countercurrent may be a response to the large discharge of fresh water during the summer from the Gambia and Senegal rivers.

Hughes and Barton (1974) found evidence of a northward flow at a depth of about 250 m extending from Cap Vert to Cabo Bojador. This poleward undercurrent was indicative of a narrow stream of cool, low salinity water flowing parallel to the continental shelf edge.

Benguela Current System

The major large-scale geostrophic currents off southwest Africa are the equatorward flow between lat. 35°S and about lat. 20°S, which is called the Benguela Current, and the primarily westward flowing Agulhas Current, which flows along the coast of south Africa to approximately long. 20°E where it is deflected to the south and east by the confluence with the west wind drift. A portion of the flow continues toward the northwest around Cape Agulhas and feeds a semi-permanent coastal jet between Cape Agulhas and Cape Columbine (Bang and Andrews, 1974). The principal features of the Benguela Current are described by Hart and Currie (1960).

The Benguela Current consists of the cool upwelled water found within 150 km of the west coast between lat. 15°S and 34°S (Shannon, 1970). In general, it flows northward, roughly following the isobaths between lat. 34°S and 23°S, while north of lat. 23°S it tends to veer away from the coast. Closer inshore a southward moving countercurrent has been occasionally recorded. Hart and Currie (1960) deduced the presence of a southward undercurrent on the continental slope off the Namibian coast from the downwarping of the mid-depth isopycnal surfaces as they approached the continental slope.

The existence of a relatively permanent cyclonic circulation over the continental slope and shelf regions between Cape Frio and a point just south of Lüderitz has been noted by Nelson and Hutchings (MS). The cyclonic circulation is comprised of the northwesterly jet-like flow southwest of Lüderitz where the flow of the Benguela Current accelerates towards the gap in the Walvis Ridge, and a southward return flow near the coast between Cape Frio and Lüderitz. The southward flow near the coast below 30 m has been reported by many investigators. Surface dynamic topography patterns from a series of monthly hydrographic cruises in this area in 1959-61 showed many instances of cyclonic gyres in the region between lat. 25°S and 20°S and southward geostrophic flow north of Lüderitz during spring and summer (Stander, 1964).

DISSOLVED OXYGEN

Minimum oxygen layers are associated with eastern boundary currents. These minimum layers are shallowest and most pronounced in the lower latitudes and more extensive and pronounced in the Pacific than in the Atlantic (Figs. 3, 4). For large-scale comparison of dissolved oxygen and its relationship to the upper mixed layer we developed annual dissolved oxygen and density (sigma-t) sections from data summarized by l-degree squares. The sections are situated several degrees offshore to allow continuous deep-water sections. This procedure introduces some bias in relation to smaller scale, nearshore features. For example, coastal upwelling or other circulation processes may result in intrusions of low oxygen water into shallower depths on the shelf, which are not indicated by our offshore sections. These intrusions are most likely to occur in the lower latitude areas which are closer to the low oxygen sources. Such intrusions have been reported in the Benguela (Stander and de Decker, 1969) and Peru Currents (Guillén, 1980).

In the California, Canary, and Benguela Currents the minimum oxygen level is altered significantly in the vicinity of the subtropical convergences. The low latitude boundaries of these regions are marked by sharp sigma-t gradients associated with the subtropical convergences (Figs. 5, 6). They occur at about lat. 3°S in the Peru Current, lat. 17°S in the Benguela Current, lat. 22°N in the Canary Current, and lat. 25°N in the California Current. The upwelling regions of the eastern boundary currents are also apparent in the density sections; there are few sigma-t surfaces intercepting the surface in the upwelling regions. Equatorward of the convergences there is a sharp dissolved oxygen gradient associated with the thermocline and low dissolved oxygen values occur very near the surface. In the Canary and Benguela systems the minimum oxygen layers deepen and disappear in the vicinity of the subtropical convergences (i.e., at about lat. 20°N and 20°S). In the California Current system the minimum oxygen layer deepens significantly near the subtropical convergence; however, an extensive minimum oxygen layer extends throughout the entire system. Throughout the California Current system low oxygen levels (i.e., less than 2 mL L^{-1}) occur at about 300 m and the oxygen minimum layer occurs at 700-900 m.

The Peru Current is significantly different from the other three currents with respect to dissolved oxygen. The subtropical convergence occurs much closer to the equator and the low oxygen layer expands and shoals in the vicinity of the convergence. The oxygen minimum is at about 300 m throughout the Peru Current system. Off Chimbote, very low dissolved oxygen levels occur just beneath the upper mixed layer. However, at Coquimbo oxygen concentrations of 2 mL L^{-1} occur at about 300 m; this is similar to the California Current situation.

Low oxygen concentration could affect reproduction of pelagic fishes through reduction of growth rates of either larvae or adults (Pauly, 1981). It could also increase mortality rates by concentrating the adults or larvae to narrow layers near the surface where they might be more susceptible to predation. However, the "worst" dissolved oxygen conditions occur in the spawning areas of the Peruvian stocks which, at least in the case of Engraulis, lie in the most productive region. The other areas most likely to be influenced by low oxygen concentrations are the spawning areas of the Namibian stocks near Palgrave Point in the Benguela Current, and the Chilean stock, which has spawning grounds near Arica. These two areas are the next most productive regions after Peru.

We see two possible explanations for the association of low oxygen concentration and high pelagic fish productivity. Low oxygen concentration is associated with high nutrient concentrations. Low oxygen concentrations near the thermocline might therefore be associated with high primary production; more primary production, hence more fishery production. The other explanation concerns competition. Extensive egg and larval surveys have been made off Peru and California. Ahlstrom (1965) showed that mesopelagic fishes and hake accounted for about 22 percent and 17 percent, respectively, of the total larvae taken off California during the 1955-58 surveys. Both mesopelagic fishes and hake have their greatest abundance below the thermocline (Ahlstrom, 1959). Off Peru mesopelagic fishes and hake comprised only 4.1 and 0.37 percent of the larvae taken during 1966-68 (Santander and de Castillo, 1979). Anchovy larvae comprised 37 percent of the larvae in the California surveys and 92 percent in the Peruvian surveys. The very low oxygen levels just beneath the thermocline off Peru would be expected to severely limit the habitat space for hake and mesopelagic fishes. Habitat space for mesopelagic fishes in the California and Canary systems and most of the Benguela system is extensive and large stocks in these areas would be expected to be in competition with epipelagic fishes for food.

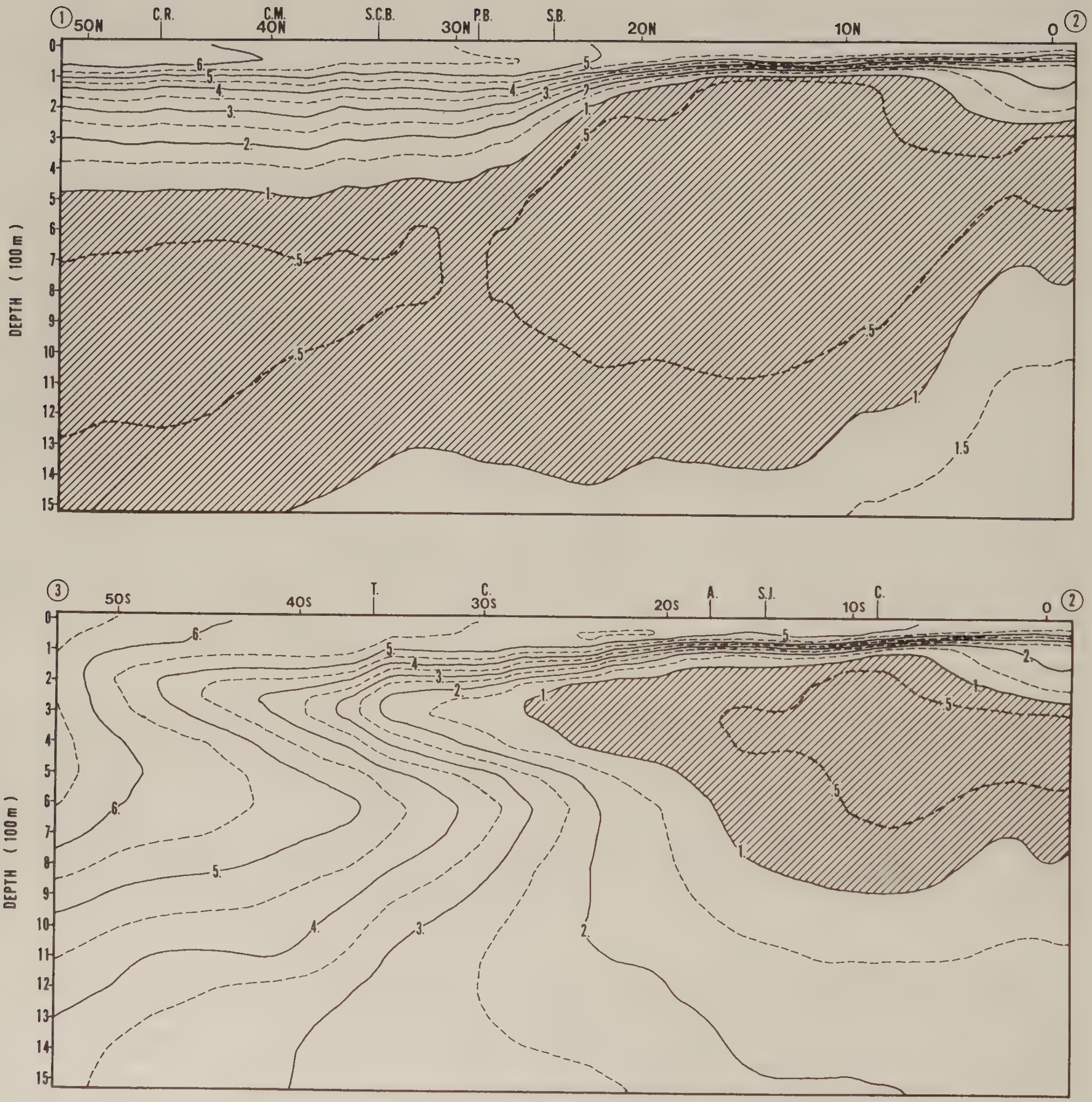


Figure 3. Dissolved oxygen (mL L^{-1}) vs. depth along the eastern boundary of the Pacific Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

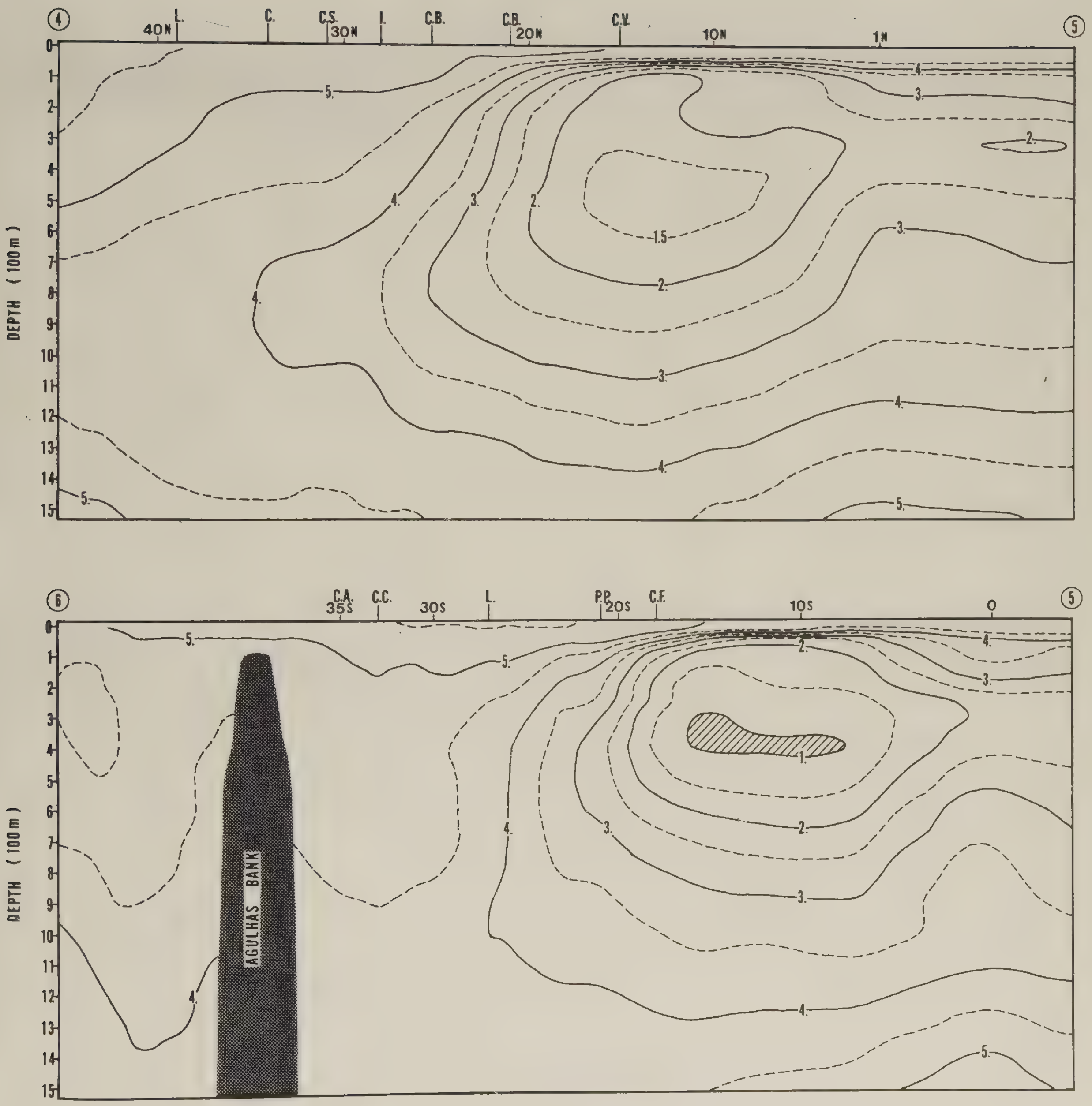


Figure 4. Dissolved oxygen (mL L^{-1}) vs. depth along the eastern boundary of the Atlantic Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

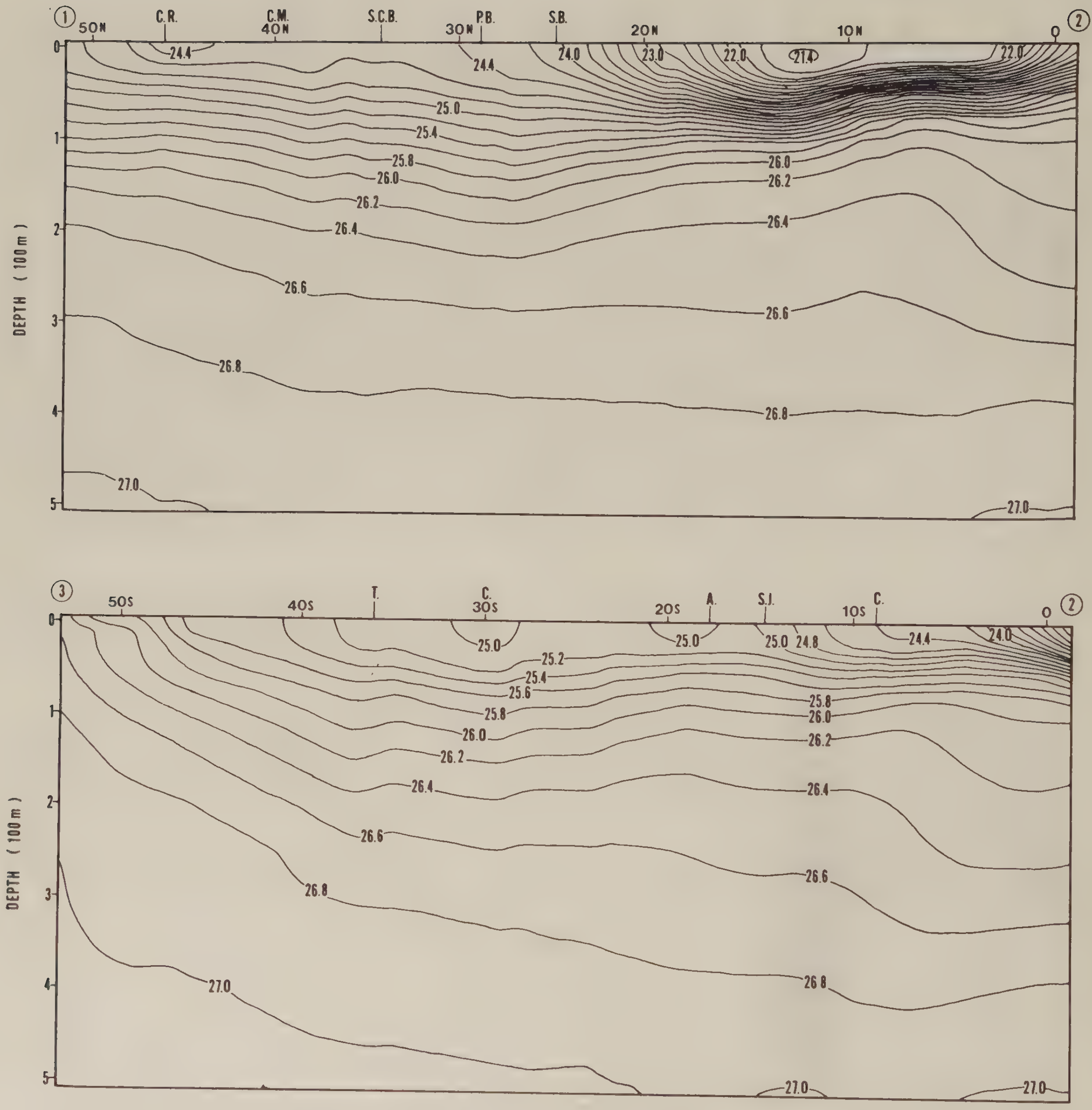


Figure 5. Sea water density (sigma-t) vs. depth along the eastern boundary of the Pacific Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

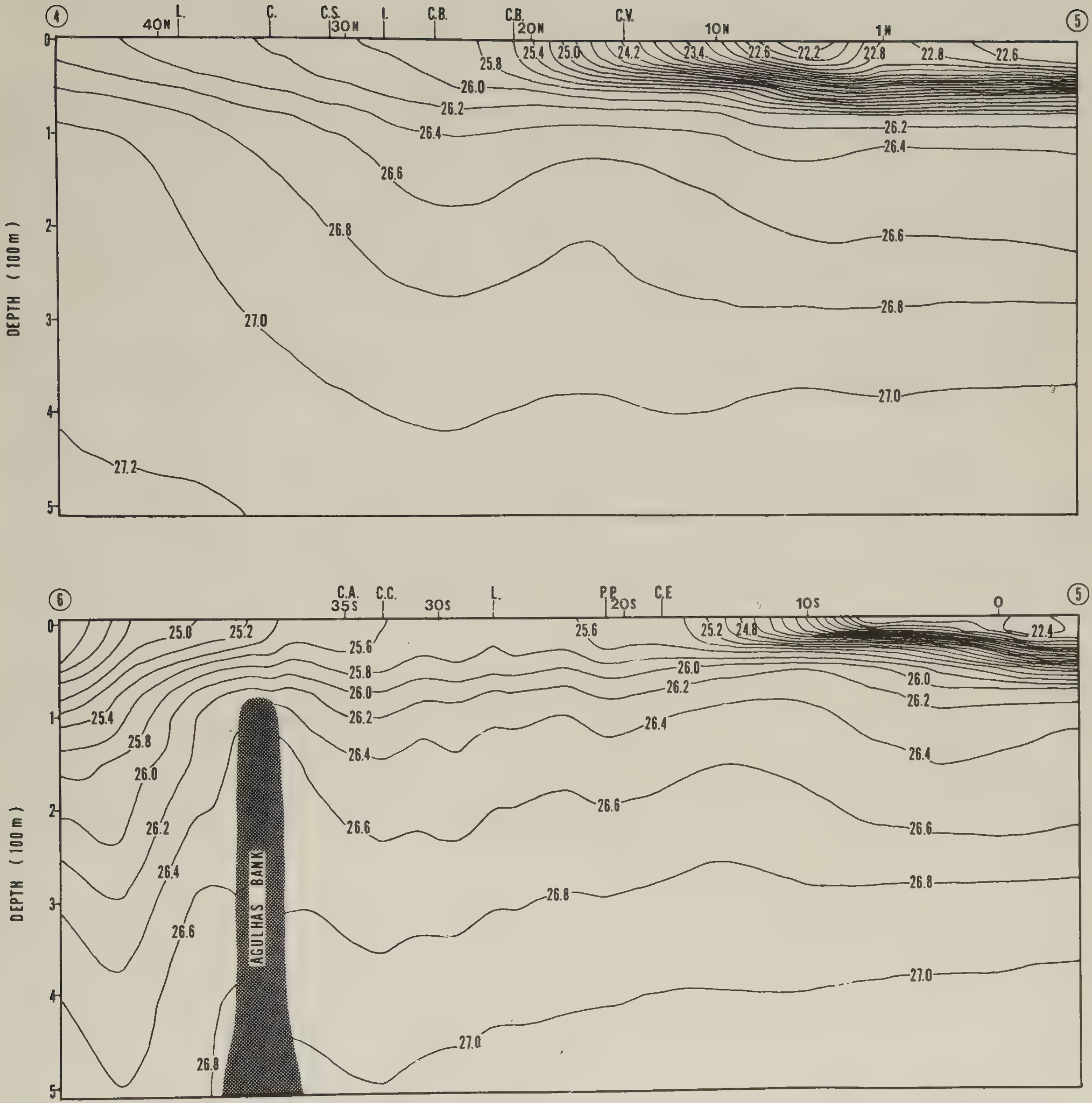


Figure 6. Sea water density (sigma-t) vs. depth along the eastern boundary of the Atlantic Ocean. The orientation of the section is shown in Figure 1. Lines at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

SUBREGIONAL ASPECTS

The charts presented in the appendix are a subset of a considerable volume of material produced and examined in this study. In order to make "cuts" of this material for presentation we have chosen several fixed locations in each eastern boundary region which appear to exemplify the range of environmental characteristics encountered in the near-coastal environments. These locations are labeled in terms of a recognizable feature of coastal geography (i.e., a coastline feature or a coastal city) and appear on the appendix maps and on Figure 7, and are listed in Tables 2 to 6.

Tables 2 and 3 briefly summarize information available on the geography and seasonality of sardine and anchovy spawning in the four eastern boundary current systems. The quality and quantity of information available varies widely among regions and within regions. Thus a fully consistent and complete synthesis is not available to us at this point. Tables 2 and 3 thus should not be considered to be "hard" data, and should not be cited as authority. They are presented as aids to recognition of patterns in the environmental summaries we have assembled (i.e., from the point of view of exploratory data analysis and hypothesis generation rather than of hypothesis testing). Our attempt at preliminary synthesis is intended to generate feedback from workshop participants and others with more specific knowledge of local situations. A discussion of the background and references to Tables 2 and 3 for the California and Peru systems are available in Bakun and Parrish (1982); major references for the Canary system are Bravo de Laguna, Fernandez, and Santana (1976), FAO (1978), and Belvèze and Bravo de Laguna (1980); major references for the Benguela system are King (1977), LeClus (1979), Badenhorst and Boyd (1980), Crawford (1980), and Crawford, Shelton, and Hutchings (1980).

Table 4 lists characteristic sea surface temperature values for 2-month segments of the annual cycle. These values were selected from bimonthly maps of long-term mean summaries which are described in the Appendix and from similar displays of the standard errors of the estimated mean values, in such a way as to characterize the shoreward 50 km of ocean or the locality over which spawning occurs. For example, in the Columbia River Plume, spawning occurs at distances of 100 km or more from the coast and so our presentations attempt to reflect conditions at that location, rather than directly adjacent to the coast.

Figure 7 displays the offshore component of surface Ekman transport plotted against the cube of the wind speed (indicating the rate of addition of turbulent mixing energy to the water column). Table 5 lists values of mixed layer depth obtained from bathythermograph data (Husby and Nelson, 1982). Sparsity of available data restricts this presentation to the California Current locations and the three northern locations in the Peru Current region. Profiles of stability structure for three Benguela locations based on hydrographic data, which lack the vertical resolution provided by bathythermograph traces, are shown in Figure 8. Table 6 contains the widths of the adjacent continental shelves.

Table 2. Spawning seasons of Pilchards
(Relative size of dots is only meaningful at each location)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.			•	•		
CAPE MENDOCINO						
S. CALIF. BIGHT	•	●	●	•		
PUNTA BAJA						
S. BAJA CALIF.	•	●	●	•	•	•

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON						
CASABLANCA	●	•	•	•	•	●
CAP SIM						
IFNI	●	•	•			●
C. BOJADOR						
CAP BLANC						
CAP VERT						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	●	●	•	•		
SAN JUAN						
ARICA	●	●	•	•	•	
COQUIMBO						
TALCAHUANO						
46°S						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO						
PALGRAVE PT.		●	•	●		
LUDERITZ						
C. COLUMBINE		●	●	●		
C. AGULHAS		●	●	●		

Table 3. Spawning seasons of Anchovies
(Relative size of dots is only meaningful at each location)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.			•	●		
CAPE MENDOCINO						
S. CALIF. BIGHT	●	●	•	•	•	•
PUNTA BAJA						
S. BAJA CALIF.	●	●	•	•	•	•

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON						
CASABLANCA						
CAP SIM						
IFNI						
C. BOJADOR			NO DATA			
CAP BLANC						
CAP VERT						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	●	●	•	•	•	•
SAN JUAN	●	•	•			
ARICA	●	●	•	•	•	•
COQUIMBO						
TALCAHUANO	●	•			•	●
46°S						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO						
PALGRAVE PT.		•	●	●	●	
LUDERITZ						
C. COLUMBINE						
C. AGULHAS		•	●	•		

Table 4. Sea Surface Temperature (°C)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.	9.2	9.5	12.6	15.1	14.7	11.3
CAPE MENDOCINO	11.0	10.6	11.1	12.1	12.9	12.1
S. CALIF. BIGHT	14.0	14.0	16.0	18.0	18.0	15.4
PUNTA BAJA	16.2	15.5	16.4	19.1	19.5	17.6
S. BAJA CALIF.	18.9	17.2	17.3	21.4	24.0	21.4

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON	14.0	14.0	16.2	18.0	18.0	15.2
CASABLANCA	16.4	16.5	18.8	22.3	21.6	18.1
CAP SIM	16.6	16.9	17.9	18.0	18.7	17.4
IFNI	17.1	17.6	18.2	19.8	20.0	18.4
C. BOJADOR	18.1	17.6	19.0	20.5	20.9	20.2
CAP BLANC	17.7	17.8	18.2	20.6	21.0	19.1
CAP VERT	19.6	19.5	23.0	27.2	27.8	24.5

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	17.6	16.9	18.5	21.3	21.1	18.6
SAN JUAN	15.6	15.1	17.3	19.6	18.1	16.7
ARICA	16.8	17.6	20.3	22.9	21.8	18.9
COQUIMBO	13.6	13.5	15.3	17.1	16.5	14.5
TALCAHUANO	12.0	12.2	14.1	14.9	14.7	13.2
46°S	8.6	10.8	11.1	13.1	12.7	9.9

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO	14.8	14.9	16.5	18.7	17.3	15.7
PALGRAVE PT.	14.8	14.2	15.0	18.6	17.6	16.1
LUDERITZ	13.0	13.0	14.0	15.0	14.0	14.5
C. COLUMBINE	14.0	14.7	16.0	16.0	15.0	15.0
C. AGULHAS	15.2	15.8	19.0	20.0	18.4	16.6

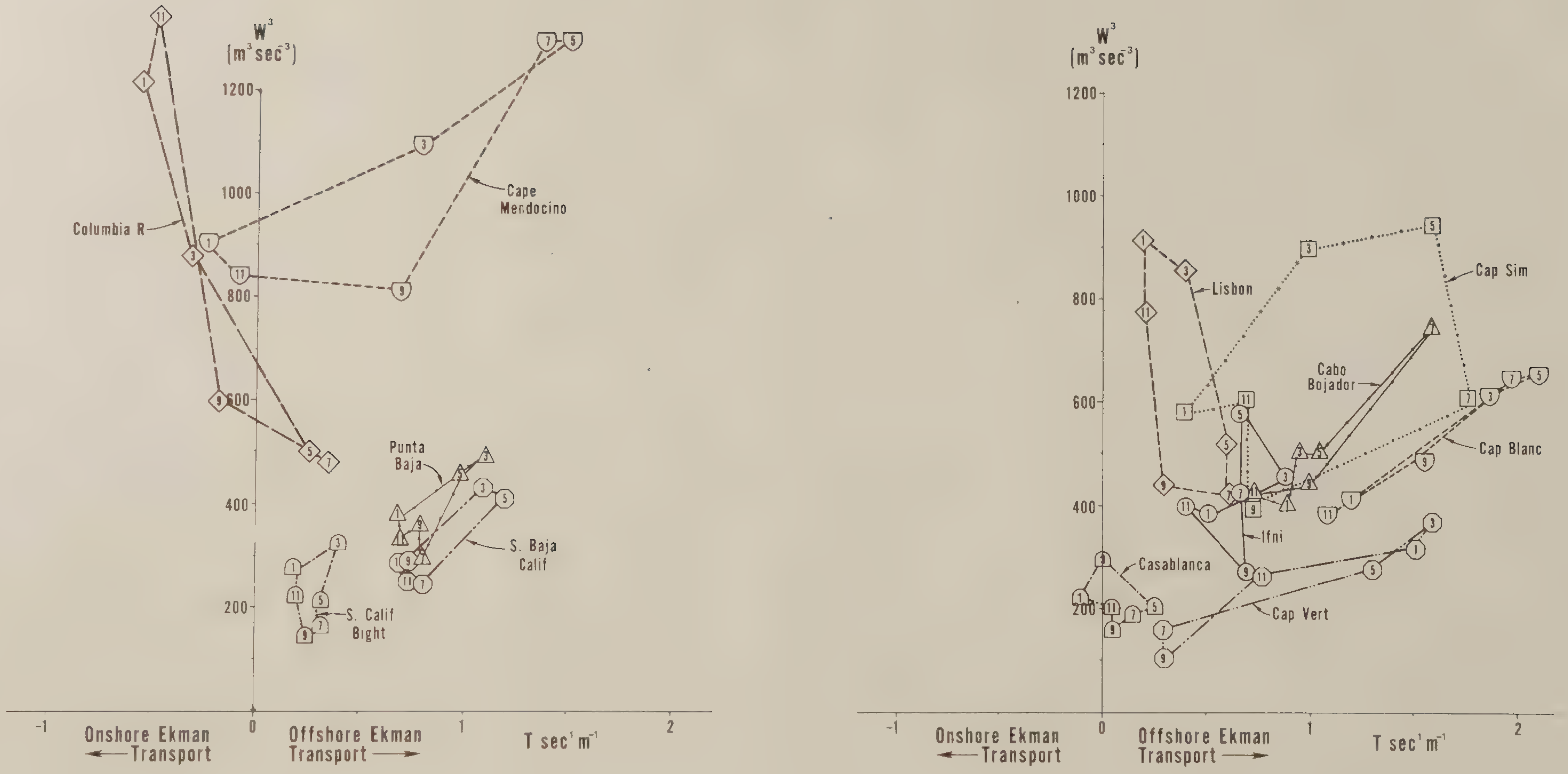


Figure 7. Characteristic seasonal relationships between W^3 (cube of the wind speed) index of turbulent mixing energy production and offshore Ekman transport at various locations in the California, Canary, Peru and Benguela Current systems. Each numbered symbol represents a 2-month climatological sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

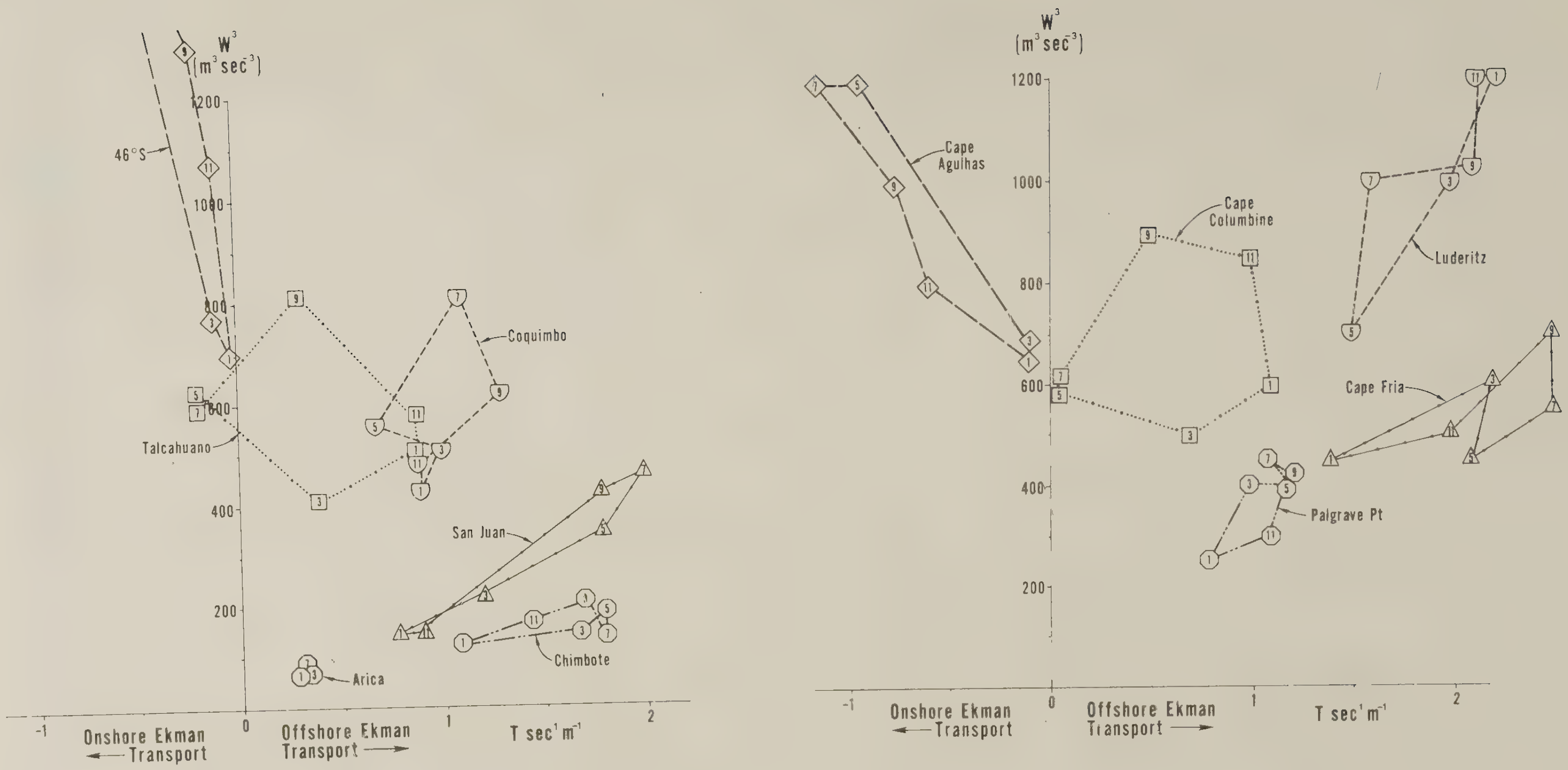


Figure 7. (continued)

Table 5. Mixed layer depths (meters) from historical bathythermograph records.

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.	103	118	10	10	16	43
CAPE MENDOCINO	-	91	42	28	54	27
S. CALIF. BIGHT	37	25	11	10	14	20
PUNTA BAJA	37	26	18	12	14	26
S. BAJA CALIF.	45	23	18	9	20	34

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	40	23	12	7	12	29
SAN JUAN	89	87	19	29	20	73
ARICA	14	18	9	5	5	10

Table 6. Approximate width* of continental shelf (km)

COLUMBIA R.	54	LISBON	43
CAPE MENDOCINO	21	CASABLANCA	56
S. CALIF. BIGHT	168	CAP SIM	38
PUNTA BAJA	29	IFNI	39
S. BAJA CALIF.	71	C. BOJADOR	40
		CAP BLANC	62
		CAP VERT	32

CHIMBOTE	132	CAPE FRIO	32
SAN JUAN	21	PALGRAVE PT.	73
ARICA	53	LUDERITZ	40
COQUIMBO	10	C. COLUMBINE	75
TALCAHUANO	44	C. AGULHAS	128
46°S	93		

*Distance from coast to 200-m contour (in the case of S. Calif. Bight, distance is to the 200-m contour at the seaward edge of the continental borderland).

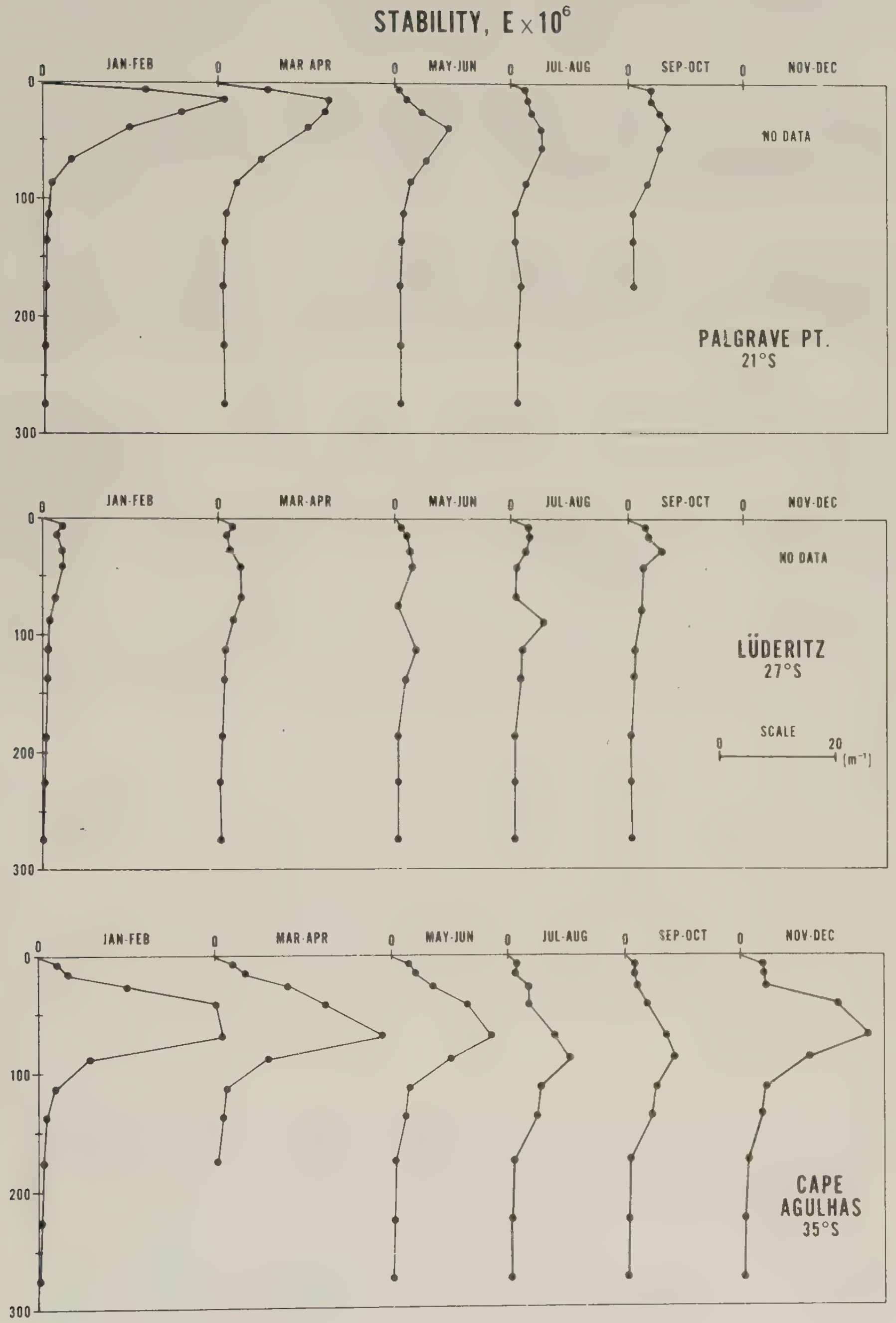


Figure 8. Static stability (m^{-1}) vs. depth for 2-month segments (for which there are sufficient hydrographic data to assemble a representative profile) of the seasonal cycles at three locations in the Benguela Current region. Depths are in meters. A scale for magnitude of stability appears to the right on the middle panel.

From these sources and the Appendix maps, the following compressed summary was constructed.

CALIFORNIA CURRENT SYSTEM

Columbia River. Anchovy spawning region (only in summer, moderate biomass); moderate continental shelf width; intense wind-generated turbulent mixing, relaxing during summer; stable upper ocean structure during summer due to lens of fresh water at the surface; onshore Ekman transport during winter--weak offshore Ekman transport during summer; little onshore-offshore temperature contrast except very near the coast.

Cape Mendocino. Primary upwelling center; narrow continental shelf; intense offshore Ekman transport, except in winter; intense turbulent mixing throughout the year; intense summer cold coastal temperature anomaly; small biomass of locally spawning fish populations; feeding grounds of adult pelagic fishes spawning elsewhere.

Southern California Bight. The major spawning grounds of pelagic fishes of the California Current; anchovy spawning region (entire year, peaking in winter-spring; large biomass); sardine spawning region (spring, pre-collapse landings 800,000 t); weak offshore Ekman transport; wide continental shelf; moderately weak turbulent mixing; relatively stable upper ocean density structure; warm coastal temperature anomalies extending very near to coast; semi-enclosed inshore gyral circulation pattern.

Punta Baja. Secondary upwelling center; narrow continental shelf; strong offshore Ekman transport, peaking in spring; moderate wind-generated turbulence; lies between two gyral circulations to the north and south and divides areas occupied by separate subpopulations of pelagic fishes. Some spawning occurs (often regarded as contiguous with Southern California Bight spawning populations). Weak negative coastal temperature anomaly.

Southern Baja California. Anchovy spawning region (winter-spring peak, moderate biomass); sardine spawning region (entire year, spring peak--moderate biomass); moderate continental shelf width; strong offshore Ekman transport; weak to moderate turbulent mixing; relatively stable upper ocean density structure; tendency for gyral circulation pattern; warm coastal temperature anomaly.

PERU CURRENT SYSTEM

Chimbote. Anchovy spawning region (spring peak, very large pre-collapse biomass); sardine spawning region (winter-spring); wide continental shelf; strong offshore Ekman transport and upwelling; weak wind-generated turbulence; very intense coastal cooling.

San Juan. Upwelling center; intense offshore Ekman transport, particularly in winter; narrow continental shelf; Turbulence level is low in summer, moderate in winter. Less stable stratification than in adjoining areas; very intense coastal cooling; reduced spawning of pelagic fishes relative to neighboring coastal areas (anchovy spawning appears to be intermediate in timing between Chimbote and Arica).

Arica. Anchovy spawning area (winter peak, large pre-collapse biomass); sardine spawning region (winter peak, large biomass); very low turbulence; weak offshore Ekman transport; moderate shelf width; extensive warm coastal temperature anomaly with a narrow band of cooling directly adjacent to the coast; gyral coastal circulation pattern.

Coquimbo. Upwelling center; intense offshore Ekman transport; extremely narrow continental shelf; cold coastal temperature anomalies extending hundreds of kilometers offshore. Turbulence level is moderate in summer, high in winter. No reported pelagic fish spawning.

Talcahuano. Seasonal upwelling (summer); moderate continental shelf width; turbulence level highest in spring; definite spatial minimum in fall and winter turbulence distributions. Anchovy spawning is reported (fall and winter only). Sardine eggs have been found.

46°S. Extreme wind-generated turbulent mixing--much higher than at the same latitude in the California Current region; no reported anchovy or sardine spawning.

CANARY CURRENT SYSTEM

Lisbon. Moderate upwelling; moderate to high wind-generated turbulence; moderately cool coastal temperature anomaly; moderate continental shelf width.

Casablanca. Sardine spawning region (peak in winter; secondary peak in summer); low turbulence levels (maximum in spring); low Ekman transport; moderate continental shelf width; slightly warm coastal temperature anomaly.

Cap Sim. Upwelling center (strongest offshore Ekman transport in summer); high wind-generated turbulence (minimum in fall); cold coastal temperature anomaly (intense in summer).

Ifni. Sardine spawning region (peak in winter, secondary peak in summer); moderate offshore Ekman transport (strongest in summer); moderate continental shelf width--shelf widens to the immediate south; local minimum in wind generated turbulence.

Cabo Bojador. Strong summer offshore Ekman transport--moderate offshore transport during the remainder of the year; fairly narrow continental shelf; turbulence levels moderate to high (summer maximum); substantial cold coastal temperature anomaly.

Cap Blanc. Upwelling center (intense offshore Ekman transport throughout the year); moderate continental shelf width; strong negative coastal temperature anomaly; moderate turbulent mixing in winter--stronger in summer.

Cap Vert. Highly seasonal upwelling; strong offshore Ekman transport in winter, relaxing greatly in summer; turbulence levels low in late summer and in fall--high in winter and spring; cold coastal temperature anomaly in winter--warm anomaly in summer. Summer and fall temperatures exceed 27°C.

BENGUELA CURRENT SYSTEM

Cape Frio. Upwelling center; intense offshore Ekman transport throughout the year, extreme in winter to early spring; strong coastal temperature gradients.

Palgrave Point. Anchovy and sardine spawning grounds (summer); substantial offshore Ekman transport (although much weaker than in the adjacent regions to the north and south--weakest in the summer); fairly wide continental shelf; weak to moderate turbulent mixing--weakest in summer (definite local minimum in the spatial distributions of wind-generated mixing energy production); stable density structure in summer.

Lüderitz. Upwelling center; very intense offshore Ekman transport; moderately narrow continental shelf; intense turbulent mixing--peak intensity in summer; intense cold coastal temperature anomaly throughout the year; low stability in the water column.

Cape Columbine. Sardine spawning grounds (summer--some anchovy spawning); seasonal upwelling; strong offshore Ekman transport in summer, vanishing in winter; moderate continental shelf width; moderate to strong turbulent mixing (spring maximum, fall minimum). A local minimum of turbulent mixing energy production lies within the coastal indentation just to the north of the cape.

Cape Agulhas. Anchovy and sardine spawning grounds (spring-summer); onshore Ekman transport; wide continental shelf; intense turbulent mixing, moderating somewhat in summer; stable ocean structure resulting from a thin lens of warm clear surface water from the Indian Ocean which overlies denser, more productive waters at depth (50-75 m).

PATTERN RECOGNITION

Our analyses of the climatological fields and information on spawning grounds suggest the following patterns. Upwelling centers, characterized by strong offshore Ekman transport, intense wind-generated turbulent mixing, reduced water column stability, and narrow continental shelves appear to be areas in which anchovies and sardines do not spawn. Spawning grounds tend to lie in coastal indentations where wind induced transport and turbulence are reduced and continental shelf width tends to be greater. The spawning grounds of the largest populations tend to be located downstream (equatorward) of upwelling centers. Smaller populations (e.g., Columbia River, Talcahuano) are located at the poleward extreme of upwelling regions where the upwelling is highly seasonal, and spawning occurs when various circumstances may reduce the effects of offshore transport and of mixing of the surface layers by the wind.

Temperature

Sea surface temperature is a better index for establishing cold temperature tolerance than warm temperature tolerance (i.e., it is a good index of the warmest water available but colder water is always available at greater depths). The physiological response of pilchard and anchovy eggs and larvae are best known for the stocks which spawn in the Southern California Bight. Lasker (1964) has shown that pilchard eggs and larvae developed normally between 13° and 21°C; however, larval mortality increased in experiments below 14°C. Incubation time decreased with increasing temperature and early growth was greatest at 16°-17°C. Anchovy eggs and larvae developed normally at 11°C (Lasker, 1964) and early growth was greatest at 21°C in the laboratory (Kramer and Zweifel, 1970).

As long as it does not approach the physiological limits, ambient temperature, at least in so far as it is reflected in sea surface temperature distributions (Table 4 and Appendix Charts 3 and 4), does not appear to exert any obvious control on reproductive habits. For example, seasonal spawning peaks off Southern Baja California and Cape Agulhas correspond to bimonthly temperature values of nearly 19°C, while at Talcahuano peak anchovy spawning occurs in winter at 13°C, even though warmer conditions are available at other seasons. Certainly, temperature conditions exceeding physiological tolerances would preclude occurrence. For example, it is probable that no anchovy spawning would occur in winter off the Columbia River (i.e., at 9°C) even if other conditions were favorable. However, in the regions where the temperatures are within physiological limits, the particular temperature appears not to be a dominant factor in determining spawning habits.

Turbulence

Spawning rarely occurs in areas of strong turbulent mixing of the upper water column. Spawning grounds are characterized by weak to moderate values of the mean cube of the wind speed, which is an index of the rate of addition of wind-generated turbulent energy to the water column (Husby and Nelson, 1982). Spawning grounds generally lie directly within spatial minima in the W^3 (wind speed cubed) distributions (Appendix Charts 9 and 10). Spawning habitats are characterized by increased stability in the internal density structure of the upper water column (Table 5, Fig. 8) that would resist dispersion of fine-scale food strata by turbulence events related to storms.

Where spawning grounds occur in regions of moderate wind-generated turbulence, other factors influencing stability may be favorable to spawning. For example, off the Columbia River the anchovy population spawns only in the summer (i.e., directly out of phase with other California Current anchovy populations). At this season, the W^3 index falls to moderate values (Fig. 7) and the subsurface stability is enhanced by the thin lens of less dense Columbia River Plume water at the sea surface. At Talcahuano, where turbulence conditions are not greatly lessened during summer, anchovy spawning remains generally in phase with other Peru Current populations; reference to Appendix Charts 9 and 10 will show that turbulent mixing in coastal areas north of Talcahuano is actually less in the winter downwelling season than in the summer upwelling season. Off Cape Agulhas, both anchovy and pilchard populations spawn under conditions characterized by substantial wind-generated mixing. However, this is a situation where particularly strong internal water column stability builds during the summer spawning season (Fig. 8), which may be due to an influx of warm Indian Ocean surface water (Darbyshire, 1966).

Transport

Areas of intense offshore transport conditions, where reproductive products might be lost from the vicinity of the coast, are characterized by minimum spawning of anchovies and pilchards. In many cases, the effects of transport and turbulence are confounded since strong wind driven offshore transport and strong wind-generated turbulence tend to coincide in eastern boundary upwelling systems. However, adaptations which result in the avoidance of offshore loss of reproductive products appear to be very widespread in fish species successfully inhabiting the California Current region (Parrish et al., 1981), indicating that transport must exact an important control on reproductive success. Note that in two situations where spawning takes place under relatively strong turbulent conditions (i.e., Talcahuano and Cape Agulhas) surface Ekman transport is directed onshore. In addition, Shelton and Hutchings (1982) have shown that a coastal jet between Cape Agulhas and Cape Columbine aids transport of larvae from the spawning grounds to the inshore nursery grounds. At Chimbote an enormous anchovy population has spawned in a situation characterized by strong offshore transport (Fig. 7); this situation is discussed in detail below.

DISCUSSION

The information presented in this analysis suggests that temperature, transport, and turbulence patterns greatly influence the timing and location of spawning grounds of anchovies and pilchards in eastern boundary currents. Furthermore no single feature has overriding control. It appears that individual stocks have adapted their reproductive strategies to achieve local optimum solutions to these three physical factors. We assume that this also applies to the three factors of the IREX equation which we have not addressed: food, predation, and population density. The question of how good individual optimum solutions are, is probably best judged by the size of the stocks.

The four major eastern boundary currents have a great deal in common. The locations and seasonality of maximum offshore Ekman transport appear to be closely related to the seasonal latitudinal shifts of the atmospheric pressure systems, intensification of the large-scale pressure gradients, and the relationships between these systems and the large-scale topography of the continents. However, as can be seen in the environmental features presented here, there are also large differences among them. For example, all four systems have maximum cold inshore-offshore temperature anomalies associated with summer maxima of offshore Ekman transport. These summer "maximum upwelling regions" have anchovy and/or sardine stocks with spawning grounds poleward and equatorward of them. The California and Benguela systems each have a single area with cold sea surface temperature anomalies. In the California system this area is located in the summer upwelling maximum, whereas the Benguela system's area includes the summer upwelling maximum at Lüderitz and a winter upwelling maximum at Cape Frio. The Peru and Canary systems each have two separate areas of cold sea surface temperature anomalies. The Peru system has an area located at the winter upwelling maximum (San Juan to Chimbote) and a second area in the upwelling region off central Chile which has a summer maximum near Talcahuano. The Canary system has a summer upwelling maximum off Lisbon and a second summer upwelling maximum between Cap Sim and Cap Blanc. During the winter the cold water anomaly off northwest Africa shifts south and the upwelling maximum then extends from Cap Blanc to Cap Vert.

We have noted that spawning of anchovies and pilchards does not occur in the summer upwelling maximum regions, which are characterized by extensive offshore Ekman transport and high wind speed cubed values. Summer mean sea surface temperature values in these upwelling maxima vary from 12°C at Cape Mendocino to 18°C at Cap Sim and Lisbon. Spawning grounds and different stocks generally occur "upstream" and "downstream" of these summer maxima. This suggests that one way to classify the stocks is by their location with respect to upwelling maxima.

Our three classes would be (1) stocks poleward of the summer upwelling maxima, (2) stocks equatorward of the summer upwelling maxima, and (3) stocks equatorward of the winter upwelling maxima. Note that very little is known of the stocks in the lower latitudes of the Canary Current. This classification system also works reasonably well in describing potential fishery yields. Maximum annual yields observed in the higher latitude stocks range from 100,000 to 400,000 tons. Maximum yields in the second group are between 800,000 and 2,000,000 tons. The only stock in the third group, the Peruvian anchoveta, yielded in excess of 10,000,000 tons.

The stocks with spawning grounds equatorward of the summer upwelling maxima, with the exception of the stock spawning near Palgrave Point, have a number of features in common. Their spawning grounds (i.e., the Southern California Bight, Arica, Casablanca, and Ifni) are in bights with weak offshore Ekman transport, little inshore-offshore temperature anomaly, and low wind speed cubed values. The anchovy stocks tend to spawn in the late winter - early spring and peak pilchard spawning is either at the same time or just after the anchovy peak. The Palgrave Point spawning grounds occur within an area with a cold inshore-offshore temperature anomaly and spawning in this region occurs in summer when offshore transport and turbulence are at a local minimum. Mean sea surface temperature is in the 14°-18°C range during the spawning season in all of spawning grounds.

The higher latitude stocks (i.e., those with spawning grounds near the Columbia River, Talcahauno, and Cape Agulhas) are in areas in which turbulence (wind speed cubed) varies seasonally from moderate to high. We have not analyzed the high latitude region of the Canary Current. Ekman transport is onshore during the spawning season in the Talcahauno and Cape Agulhas spawning grounds. The Columbia River region has weak offshore transport during the spawning season and onshore transport during the rest of the year. The Columbia River and Cape Agulhas stocks spawn in the summer when wind speed cubed is at a minimum and spawning occurs in areas where the stability of the water column is increased by intrusions of different water masses (e.g., Columbia River water and Agulhas Current water). The Talcahauno anchoveta stock spawns in the early winter (Jordán, 1980) instead of in the summer when sea surface temperature is at a maximum. We do not know the exact location of this stock's spawning grounds, however, a region of minimum wind speed cubed lies just north of Talcahauno in the early winter.

THE PERUVIAN ANOMALY

The anchoveta stock, spawning in the area centered near Chimbote, has been by far the largest stock in the world. We have noted that this area stands out as an anomaly among the major spawning regions in that it is characterized by strong offshore Ekman transport (Fig. 7). Several factors could conceivably be acting to minimize associated offshore loss of reproductive products from this area.

Huyer (1976) has indicated that the offshore extent of coastal upwelling regions may be expanded in regions of wide continental shelves; the continental shelf off Chimbote is much wider than off other upwelling centers (Table 6). Also, the Rossby radius of deformation, which is the intrinsic coastal boundary layer width scale (Mooers and Allen, 1973), is inversely dependent on the sine of the latitude. Thus the Rossby radius at Chimbote (lat. 9°S) is about twice that at Arica, Palgrave Point, or Cap Blanc, more than 3 times that at Coquimbo, Punta Baja, or Ifni, and about 4 times that at Cape Mendocino or Lisbon.

A more speculative set of considerations concerns the dependence of Ekman layer depth on latitude. The expression for the Ekman depth scale (Ekman, 1905) contains the square root of the sine of the latitude in the denominator. Thus, for comparable vertical eddy viscosities, the Ekman depth at Chimbote would be twice that at Cape Mendocino or Lisbon, for example. For a given magnitude of offshore transport, therefore, the corresponding average offshore velocity of the Ekman layer off Chimbote would be one-half that off Cape Mendocino or Lisbon. Opposing this effect would be the expectation that increasing turbulence input at the higher latitude locations would tend to increase the vertical eddy viscosity which is in the numerator of the Ekman depth expression.

Bakun and Parrish (1982) noted that the peak spawning off Chimbote in winter occurs during the season of strongest offshore transport and hypothesized avoidance of detrimental effects of intermittent El Niño events as a possible reason. An alternate hypothesis concerns Ekman depth which tends to be limited by sharp density discontinuities due to inhibition of vertical eddy viscosity, such that the layer above the discontinuity tends to slide over the denser lower layer which will be relatively unaffected (Neumann and Pierson, 1966, p. 196). The mixed layer depth (Table 5) off Chimbote is much less (7 m) during summer than in winter (40 m). Averaging the corresponding summer (1.1 $m^2 sec^{-1}$) and winter (1.8 $m^2 sec^{-1}$) Ekman transports (Fig. 7) over these depth layers yields average offshore Ekman speeds of approximately 0.04 m sec^{-1} (3.5 km d^{-1}) in winter and 0.16 m sec^{-1} (14.0 km d^{-1}) in summer. Planktonic reproductive products within the mixed layer would thereby be dispersed offshore four times as rapidly during summer than during the winter spawning peak.

IMPLICATIONS FOR POPULATION MODELING

Fishery time series are generally quite short and often contain only one to several realizations of major shifts in trend (e.g., Fig. 2). The result is that there are often insufficient degrees of freedom for purely empirical approaches to be effective in defining relationships with multiple environmental factors. Thus it is important to incorporate as much accessory information as can be gleaned independently from the actual time series data. Accessory information can come from process-oriented experiments or from various deductive approaches such as the one we have presented in this paper.

The most straightforward way to incorporate this sort of information is in the choice and formulation of the explanatory variables. By choosing a very limited set of variables which addresses only those processes which appear to be the most crucial and by formulating these variables specifically according to the manner in which they appear to affect the populations, the degrees of freedom available in the time series can be expended with the greatest likelihood of generating beneficial information (Bakun and Parrish, 1980).

In this study we have compared seasonality and geography of reproduction with corresponding features in the environment. Since natural selection implies adaptation of reproductive strategies to the most crucial processes affecting reproductive success, patterns of correspondence may illuminate the environmental linkages.

We have noted that spawning tends not to occur in regions characterized by wind conditions which would generate intense turbulent mixing of the upper water column. This would tend to support Lasker's (1978) mechanism for larval mortality caused by wind-generated turbulent dispersion of fine-scale strata of food particles appropriate for first-feeding. Some degree of information on surface wind conditions is generally available. In view of the hypothesized mechanism, the average turbulence generation over monthly or longer intervals is probably not the ideal way to formulate this variable. Rather, the frequency and duration of periods where wind speeds do not exceed a critical threshold, above which it would breakdown the underlying water column stability, may be more pertinent considerations (Husby and Nelson, 1982). No specifics of such a formulation have been proposed.

Another pattern in reproductive strategies is the absence of spawning in regions characterized by strong offshore transport whereby reproductive products are lost. This mechanism tends to be confounded with the turbulence mechanism in the situations we are examining. For example, in upwelling centers, strong offshore transport coincides with intense turbulence generation. However, we have noted indications that the transport mechanism is acting (i.e., in certain situations where characteristic transport is not directed strongly offshore, spawning occurs under conditions which appear to by typified by substantial wind-generated turbulence). We have also speculated that the seasonality of spawning at Chimbote is tuned so as to minimize offshore dispersion of reproductive products, rather than to minimize turbulent mixing.

As is the case for the turbulence indices, estimates of offshore Ekman transport (e.g., Bakun, 1973) can also be generated from wind information. However, the two mechanisms imply distinctly different time scales. The turbulence mechanism acts to cause larval starvation on a time scale of a few days; it is non-linear in that water once mixed is not unmixed by reversing the action of the wind. The transport mechanism acts on much longer time scales and may indirectly cause mortality of late larvae and juveniles by displacing them from the favorable coastal environments. Transport is linearly additive; a period of offshore transport could be counteracted by a later period of onshore transport.

No pattern has emerged to indicate that reproductive strategies are strongly influenced by an optimum temperature. Obviously, the physiological temperature limits of the organisms provide barriers to reproduction in extreme cases. This analysis suggests that the effective way to incorporate temperature data in an empirical recruitment model may be simply as an indicator variable which has a value of "one" for a range of temperatures within which spawning can occur and "zero" beyond that range. An additional temperature effect, which may become significant once the variance due to the indicator variable is accounted for, may occur due to increases in physiological rates, etc., by increases in temperature within the generally favorable range.

APPENDIX

OCEANOGRAPHIC DATA

To assemble characteristic distributions of the large-scale oceanographic features in the four boundary current regions, we used existing global summaries of subsurface data. Objectively analyzed fields of annual mean temperature, salinity, and oxygen at standard depths were provided by Sydney Levitus of the National Oceanic and Atmospheric Administration's (NOAA) Geophysical Fluid Dynamics Laboratory (GFDL). Data sources and analysis methods and selected horizontal distributions and vertical sections are described in detail by Levitus and Oort (1977) and Levitus (1982).

The annual mean geostrophic flow at the surface was constructed from the analyzed fields of temperature and salinity defined on a grid of 1-degree latitude by 1-degree longitude in each of the eastern boundary current regions. Dynamic topographies relative to the 1000 db level (approximately 1000 m) were computed following LaFond (1951). The computation points for surface velocity are offset from the values of dynamic height by a half-degree in both directions (i.e., calculated velocities are centered on the whole degree of latitude and longitude). Therefore, a velocity vector for each 1-degree square was calculated from the gradients defined by dynamic height values at the corners of each square. To clarify the presentations shown in Chart 1, vector symbols are only plotted for alternate 1-degree squares in both latitude and longitude coordinates. Contours of dynamic height (in dynamic meters, with a contour interval of 0.04 dyn m) are superimposed on the vector fields as an aid to interpreting the flow direction and strength (i.e., the surface geostrophic flow is parallel to contours of dynamic height and the current speed is inversely proportional to the contour spacing and to the sine of the latitude). Directions are defined such that higher values of dynamic height lie to the right (left) of the current in the northern (southern) hemisphere when facing in the direction of flow.

The analyzed fields from which these velocity calculations have been made were designed for global, rather than regional studies of ocean circulation. Well recognized seasonal variations in surface current features are not depicted in the annual mean distributions. For example, where speeds represented in Chart 1 vary from 2 to 10 cm sec^{-1}, typical seasonal ranges may be up to an order of magnitude larger. The results are rather smooth representations in which much of the temporal and spatial detail available in finer scale summaries (Wyllie, 1966; Hart and Currie, 1960; Robles, 1979) has been filtered out. No attempt has been made to extrapolate the dynamic height calculations into shallow coastal regions (i.e., bottom depths less than 1000 m). Where these summaries do not depict major circulation features near the coast, the predominant flow directions have been indicated by shaded arrows (e.g., over the Agulhas Bank and in the Southern California Bight).

Characteristic vertical sections of oxygen (Figs. 3,4) and density (Figs. 5,6) along predominantly meridional axes of the eastern boundary current systems were also constructed from the large-scale analyses. The locations of the sections are shown in Figure 1. Although the sections lie up to several hundred kilometers from the coast, the general features (e.g., oxygen minima) are felt to be representative of the coastal regimes, as well. Values of oxygen (mL L^{-1}) defined at standard depths between the surface and 1500 m are contoured with an interval of 0.5 mL L^{-1}. Oxygen minima (values less than 1.0 mL L^{-1}) are indicated by cross-hatching. Analogous sections of density (sigma-t) were derived from the annual mean values of temperature and salinity in the upper 500 m of the water column. Values of sigma-t are contoured with an interval of 0.2. On each vertical section, the latitudinal locations associated with prominent coastal features (e.g., capes and coastal cities) are designated by simple letter abbreviations. The reader is directed to Figure 1 and to Chart 1 for proper orientation of each section.

Historical mechanical bathythermograph (MBT) profiles and hydrocast data (temperature and salinity versus depth) archived in the Master Oceanographic Observation Data Set (MOODS) at the U.S. Navy's Fleet Numerical Oceanography Center (FNOC) in Monterey, California were used to calculate indices of mixed layer depth (Table 5) and selected profiles of vertical stability (Fig. 8). Mixed layer depths (in meters) were defined and calculated as described by Husby and Nelson (1982). The vertical gradient of sigma-t was used as an index of the static stability (E) of the water column, as suggested by Hesselberg and Sverdrup (1915; cited in Sverdrup, Johnson, and Fleming, 1942). Bimonthly vertical profiles of static stability ($E \times 10^{6}$ m^{-1}) in the upper 300 m are displayed for three locations in the Benguela Current system (Fig. 8).

SURFACE MARINE DATA

The climatological distributions of sea surface temperature, coastal-oceanic temperature contrast, surface layer Ekman transport, wind-generated turbulent energy production, and total cloud amount presented in this appendix are based on summaries of data contained in the National Climatic Center's (NCC) file of surface marine observations (Tape Data Family-11). The total file contains in excess of 50 million individual ship reports dating from the mid-19th century through 1979. Over 3.3 million of the reports are from the area of the Canary Current system. Summaries for the California and Benguela Current regions are based on 1.9 million and 1 million individual reports, respectively. The area off western South America contains an order of magnitude fewer surface weather observations (0.3 million).

Long-term composite summer and winter distributions of surface atmospheric properties were compiled by 1-degree latitude and longitude quadrangles within the four geographical regions outlined in Figure 1. The boundaries of the summary grids are defined as follows:

1. California Current - extends from lat. 20° N to 50°N and from the coast to 15 degrees of longitude offshore.
2. Peru Current - extends from lat. 50° S to 4°S and from the coast to 14 degrees of longitude offshore.
3. Canary Current - extends from lat. 5° N to 45°N and from the coast to 15 degrees of longitude offshore.
4. Benguela Current - extends from lat. 39° S to 8° S and from long. 35° E to 2° E; off the southwest coast, the data extend from the coast to 11 degrees of longitude offshore.

In each case, the data grid parallels the coastline configuration and each 1-degree quadrilateral is centered on a whole degree of latitude and longitude. All observations available in the TDF-11 file within the summary regions were averaged over six, two-month periods. Therefore, a mean value for each two-month period and square is formed from a data set which is independent of all other months and squares. Although all six bimonthly distributions were examined, we selected the January-February and July-August fields to represent the characteristic distributions for summer and winter seasons in the respective hemispheres.

The observations contained in the TDF-11 file vary markedly in methods and precision of measurement due to the changes in instrumentation, sampling techniques, and reporting procedures over the considerable time period covered by the data base. Based on the documentation for the TDF-11 data file[4/], a single pass editor was used to remove gross errors in the data, including erroneous position reports, and observations of sea surface temperature, wind speed and direction, and cloud amount exceeding extreme value limits. Detailed discussions of the sources of measurement errors and techniques for more refined data editing may be found in Bakun, McLain, and Mayo (1974), Nelson (1977), and Nelson and Husby (1983).

The spatial distributions of surface marine observations are known to be biased to the coastwise and transoceanic shipping lanes between major seaports. Chart 2 shows the distribution of total numbers of observations per 1-degree quadrangle in each boundary current region. A contour interval of 5,000 has been used and values exceeding 10,000 observations per 1-degree square are shaded. However, note that for the Peru Current region, the contour interval is 500 and values greater than 1000 observations per 1-degree square are shaded. In most cases, the highest density of reports lies within 300 km of the coast, except off southwestern Africa, where the narrow main shipping lane diverges sharply from the coast north of Cape Columbine. The numbers of reports per 1-degree square range from fewer than 50 off Peru and Chile to more than 40,000 in the Southern California Bight and off the Iberian Peninsula. Summer and winter averages are most reliable within the well traveled shipping lanes, but less precise in the offshore regions. Some temporal bias may also exist, since approximately 60-80 percent of the total reports have been taken since 1950.

[4/] National Climatic Center, Tape Data Family 11, NOAA/EDIS/NCC, Asheville, N.C.

The composite distributions are based on independent 1-degree square sample means. Detail within a single square which is not supported by similar values in surrounding squares reflects sampling error. Therefore, when contoured fields have been used to display the results of this study, the mean distributions have been machine contoured, subjectively smoothed, and recontoured to remove extreme values which were not supported by data in directly adjacent squares. Typically, "bull's-eyes" in the contoured fields reflected a paucity of ship observations or inadequate sampling of extreme events.

Sea Surface Temperature- Charts 3 and 4

Summer and winter distributions of sea surface temperature (°C) are contoured at intervals of 1°C. Seasonal cycles of sea surface temperature at selected coastal locations in each boundary current are listed in Table 4.

Coastal Temperature Anomaly - Charts 5 and 6

Summer and winter distributions of coastal temperature anomaly were constructed from the corresponding fields of sea surface temperature as follows. A smoothed offshore temperature reference was constructed by successively applying, at each 1-degree latitude increment, a 5-degree latitude by 3-degree longitude moving-average filter centered at the tenth 1-degree square from the coast. Sampling irregularities were reduced by discarding the three highest and three lowest values of the fifteen sample averages covered by the filter at each step, and averaging the remaining nine values. The value of this offshore reference temperature at the proper latitude was subtracted from each 1-degree averaged sea surface temperature. The coastal temperature anomaly, therefore, is the difference between the sea surface temperature at each location and the large-scale temperature offshore. The method is similar to that used by Böhnecke (1936; cited in Wooster and Reid, 1963) to describe the Canary Current and Benguela Current upwelling systems, in that it attempts to filter the basin-wide meridional temperature gradient, thereby highlighting local effects.

Temperature anomalies (°C) are contoured with an interval of 1°C. Anomalies less than -2°C are shaded. Cross-hatching designates positive anomalies greater than 1°C. Negative anomalies indicate that the mean sea surface temperature is colder than the offshore reference temperature; positive values indicate the opposite.

Ekman Transport - Charts 7 and 8

Surface wind reports from the TDF-11 data file were used to construct summer and winter distributions of surface layer Ekman transport in each of the eastern boundary current regions. Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter, and is directed 90° to the right (left) of the surface wind stress in the northern (southern) hemisphere. The method of calculation is described by Bakun et al. (1974). To clarify the presentations, vector symbols are only plotted for alternate 1-degree squares in both latitude and longitude coordinates. Ekman transport is plotted in units of metric tons per second per meter (t sec^{-1} m^{-1}), and vector symbols are scaled according to the key on the charts.

Scatter diagrams of Ekman transport versus the cube of the wind speed (Fig. 7) are used to distinguish between regimes characterized by strong surface layer transport and those dominated by wind-generated turbulence. At selected locations along each coast, vector means were resolved into components perpendicular and parallel to the coast. Coastline angles were determined by visually fitting a line to the dominant trend of the coast. Estimates of the offshore (onshore) directed component of Ekman transport are plotted against the cube of the wind speed in Figure 7.

Wind Speed Cubed - Charts 9 and 10

The rate at which turbulent kinetic energy of the wind is added to the upper ocean and becomes available to mix the stable thermocline layers is proportional to the third power, or "cube" of the wind speed (Niiler and Kraus, 1977). Mean summer and winter distributions of the cube of the surface wind speed were compiled from the TDF-11 surface wind reports following the methods of Husby and Nelson (1982). Mean values are plotted in units of 1000 m^3 sec^{-3} and contoured with an interval of 250 m^3 sec^{-3}. One-degree means of wind speed cubed at selected locations in each boundary current are plotted against offshore (onshore) Ekman transport in Figure 7.

Total Cloud Amount - Charts 11 and 12

Mean distributions of total cloud amount were assembled from the TDF-11 data file following procedures modified from Nelson and Husby (1983). Mean values are plotted in units of tenths of sky obscured and the contour interval is one-tenth. Based on the general patterns of cloud cover, certain inferences may be made about the expected distributions of net insolation. In particular, it should be noted that the summer distributions (Chart 11) show relative cloud cover minima at coastal locations characterized as centers of upwelling (e.g., Cape Mendocino, Cap Blanc to Cabo Bojador, Talcahuano, and Cape Columbine to Lüderitz). One implication of these distributions is that higher levels of incoming shortwave radiation reach the sea surface in the highly productive upwelling regions than elsewhere in the eastern boundary current systems (Bakun and Nelson, 1977; Nelson and Husby, 1983).

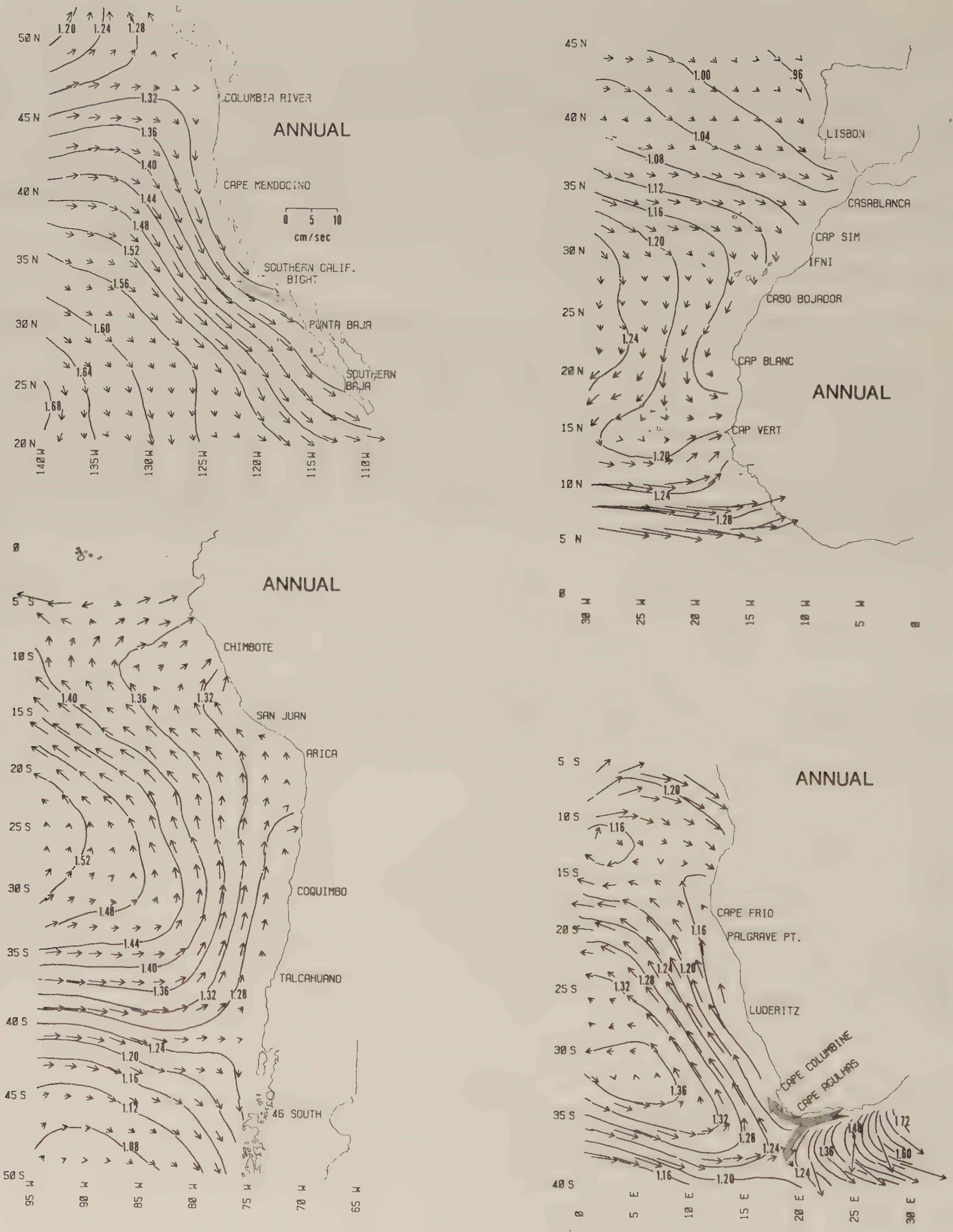

ANNUAL
COLUMBIA RIVER
CAPE MENDOCINO
0 5 10
cm/sec
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
1.20
1.24
1.28
1.32
1.36
1.40
1.44
1.48
1.52
1.56
1.60
1.64
1.68
ANNUAL
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
1.00
.96
1.04
1.08
1.12
1.16
1.20
1.24
1.20
1.24
1.28
ANNUAL
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
1.40
1.36
1.32
1.52
1.48
1.44
1.40
1.36
1.32
1.28
1.24
1.20
1.16
1.12
1.08
ANNUAL
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E
1.20
1.16
1.16
1.24
1.20
1.32
1.28
1.36
1.32
1.28
1.24
1.16
1.20
1.24
1.36
1.48
1.72
1.60

Chart 1. Annual mean surface geostrophic flow (0/1000 db, cm $\sec^{-1}$) and dynamic topography (dyn m).

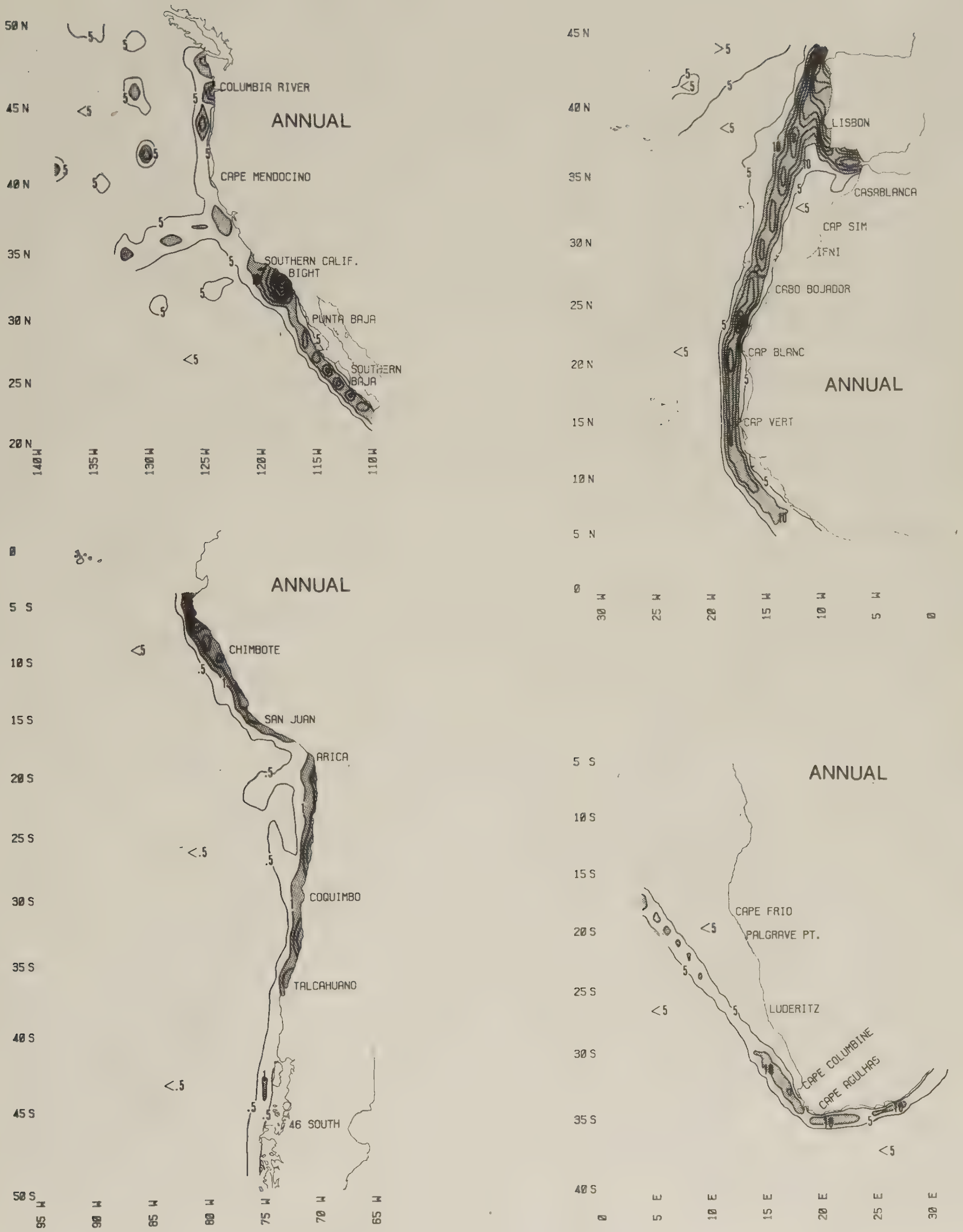

ANNUAL
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
<5
5
ANNUAL
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
>5
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
<5
5
10
ANNUAL
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
<5
<.5
.5
ANNUAL
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
<5
5
10

Chart 2. Distributions of observations per 1-degree square (thousands of observations)

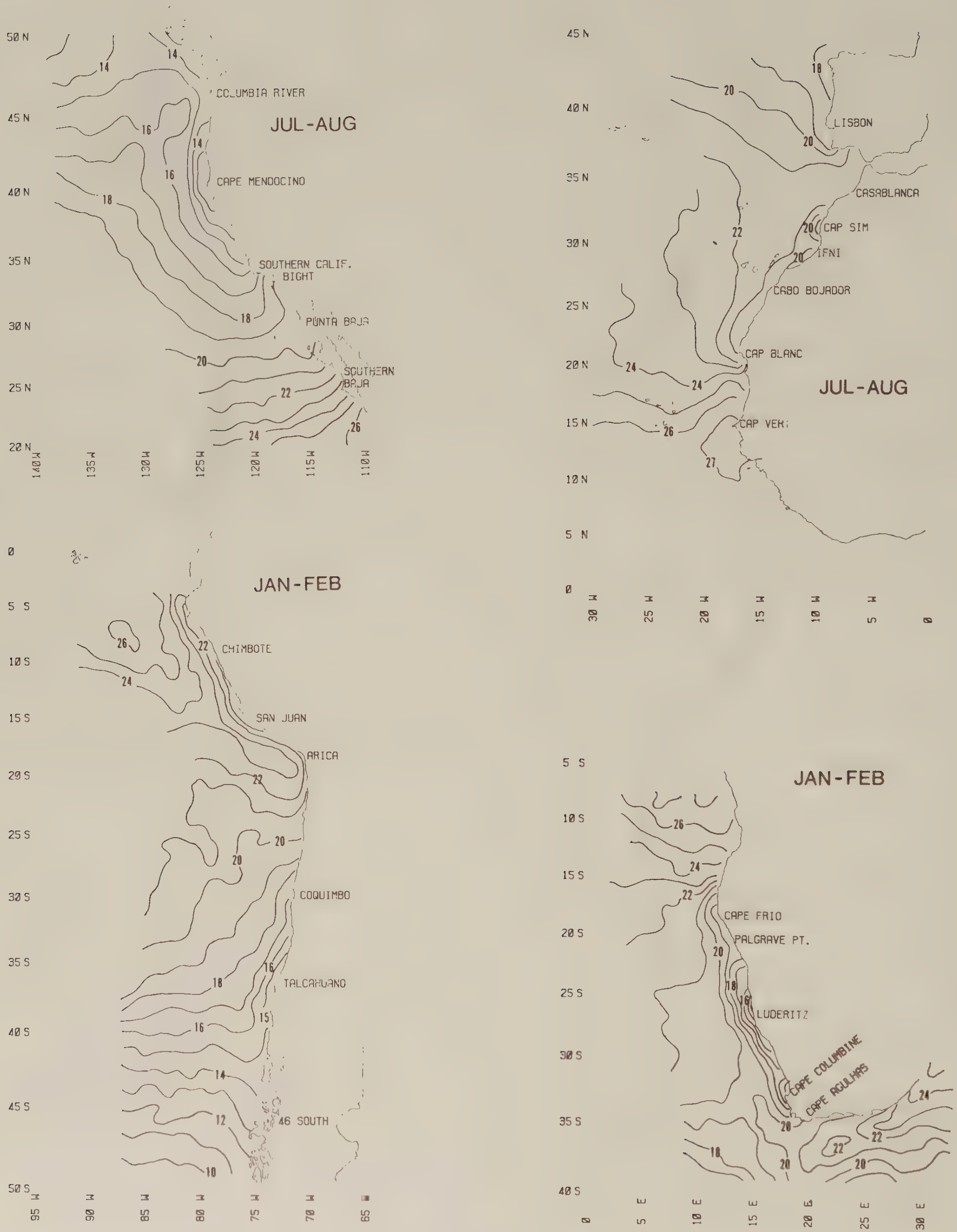

JUL-AUG
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
14
16
18
20
22
24
26
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
JUL-AUG
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
18
20
22
24
26
27
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
JAN-FEB
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
26
24
22
20
18
16
15
14
12
10
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
JAN-FEB
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E
26
24
22
20
18
16
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS

Chart 3. Summer sea surface temperature (^{o}C).

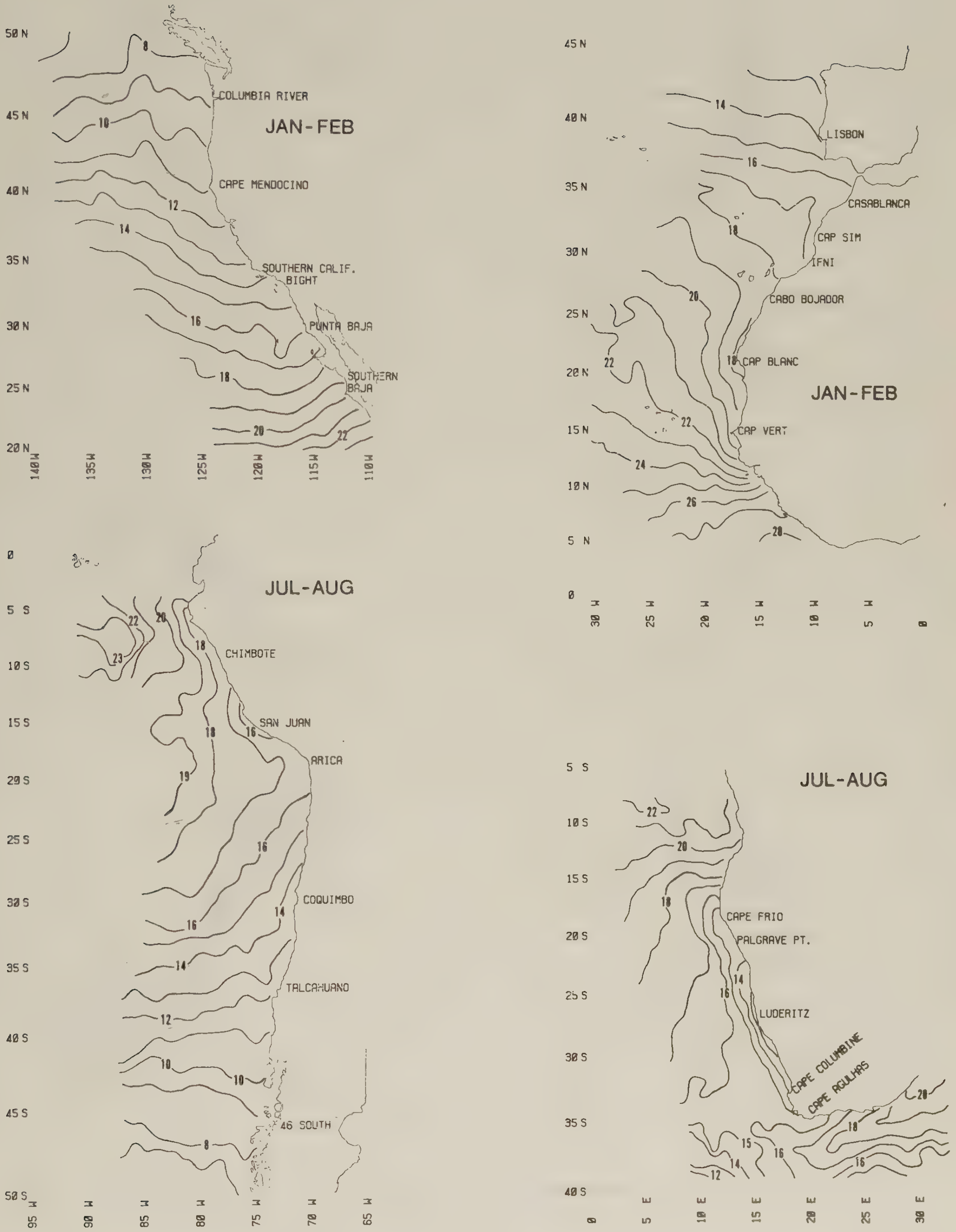

JAN-FEB
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
8
10
12
14
16
18
20
22
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
JAN-FEB
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
14
16
18
20
22
24
26
28
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
JUL-AUG
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
8
10
12
14
16
18
19
20
22
23
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JUL-AUG
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
12
14
15
16
18
20
22
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 4. Winter sea surface temperature (°C).

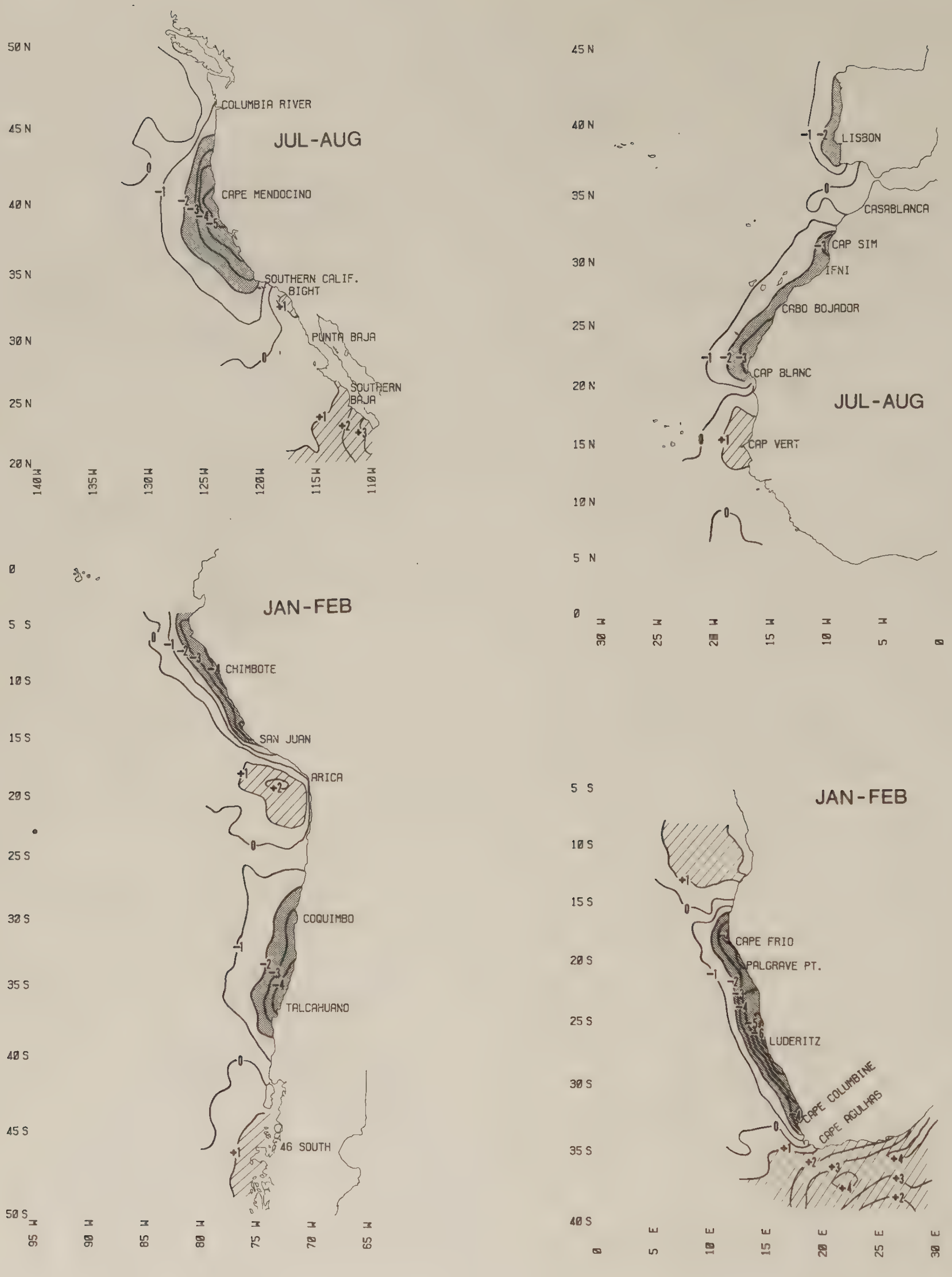

JUL-AUG
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
0
-1
-2
-3
-4
-5
+1
+2
+3
JUL-AUG
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
JAN-FEB
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JAN-FEB
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 5. Summer coastal sea surface temperature anomaly ($^{\circ}$C).

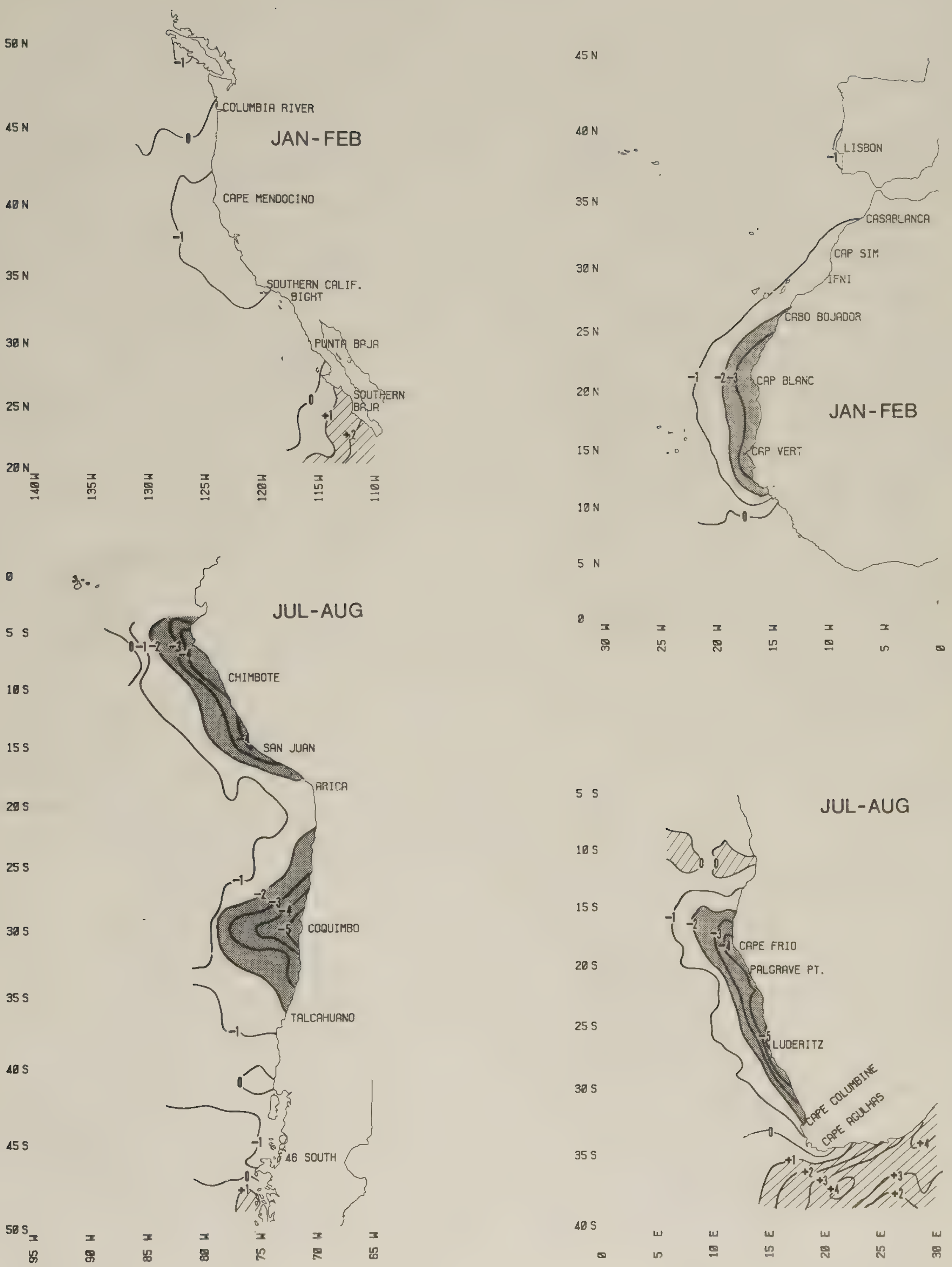

JAN-FEB
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
JAN-FEB
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
JUL-AUG
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JUL-AUG
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 6. Winter coastal sea surface temperature anomaly (^{0}C).

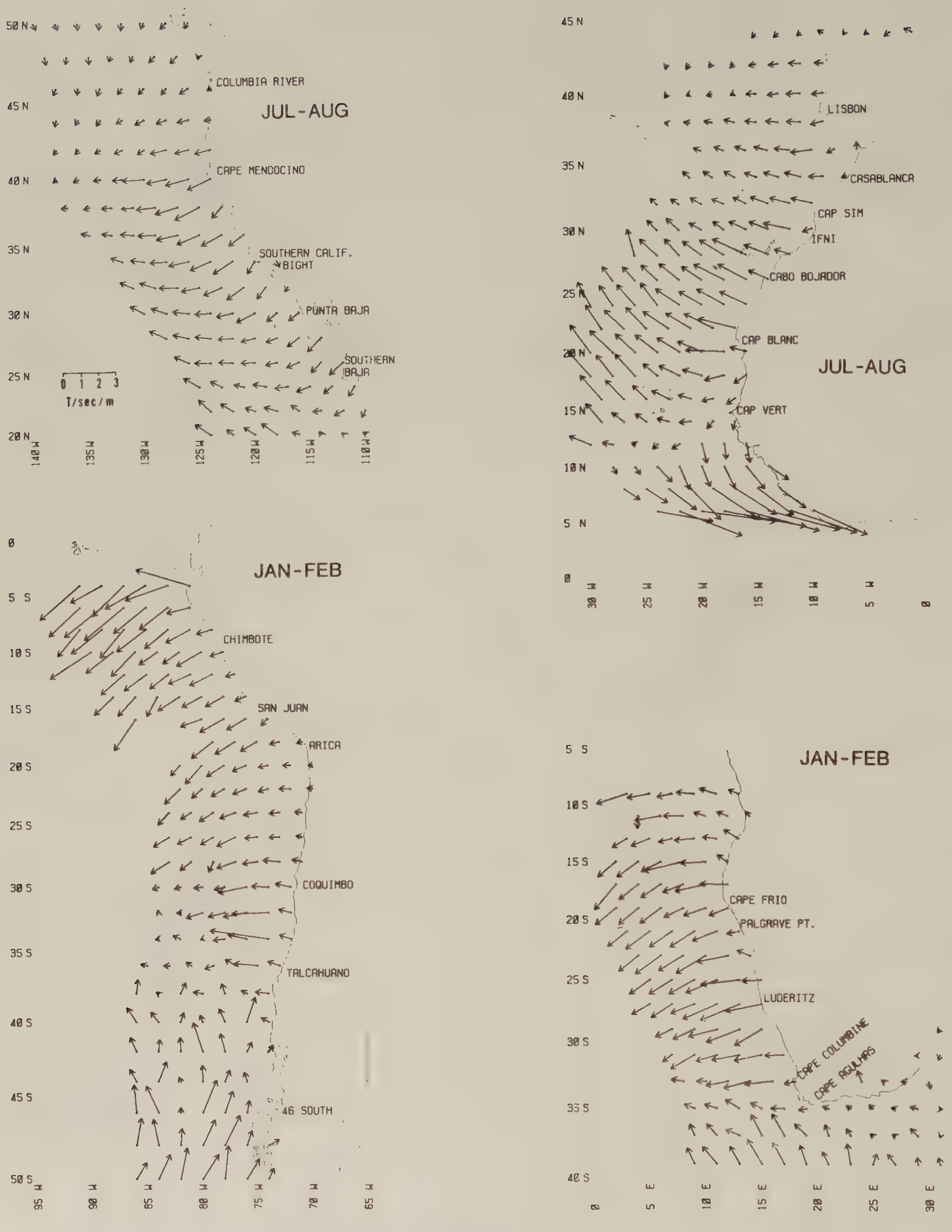

50 N
45 N
40 N
35 N
30 N
25 N
20 N
JUL-AUG
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
0 1 2 3
T/sec/m
140 W
135 W
130 W
125 W
120 W
115 W
110 W
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
JUL-AUG
CAP VERT
30 W
25 W
20 W
15 W
10 W
5 W
0
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
JAN-FEB
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
95 W
90 W
85 W
80 W
75 W
70 W
65 W
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
JAN-FEB
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 7. Summer surface Ekman transport (t $\sec^{-1}$ m^{-1})

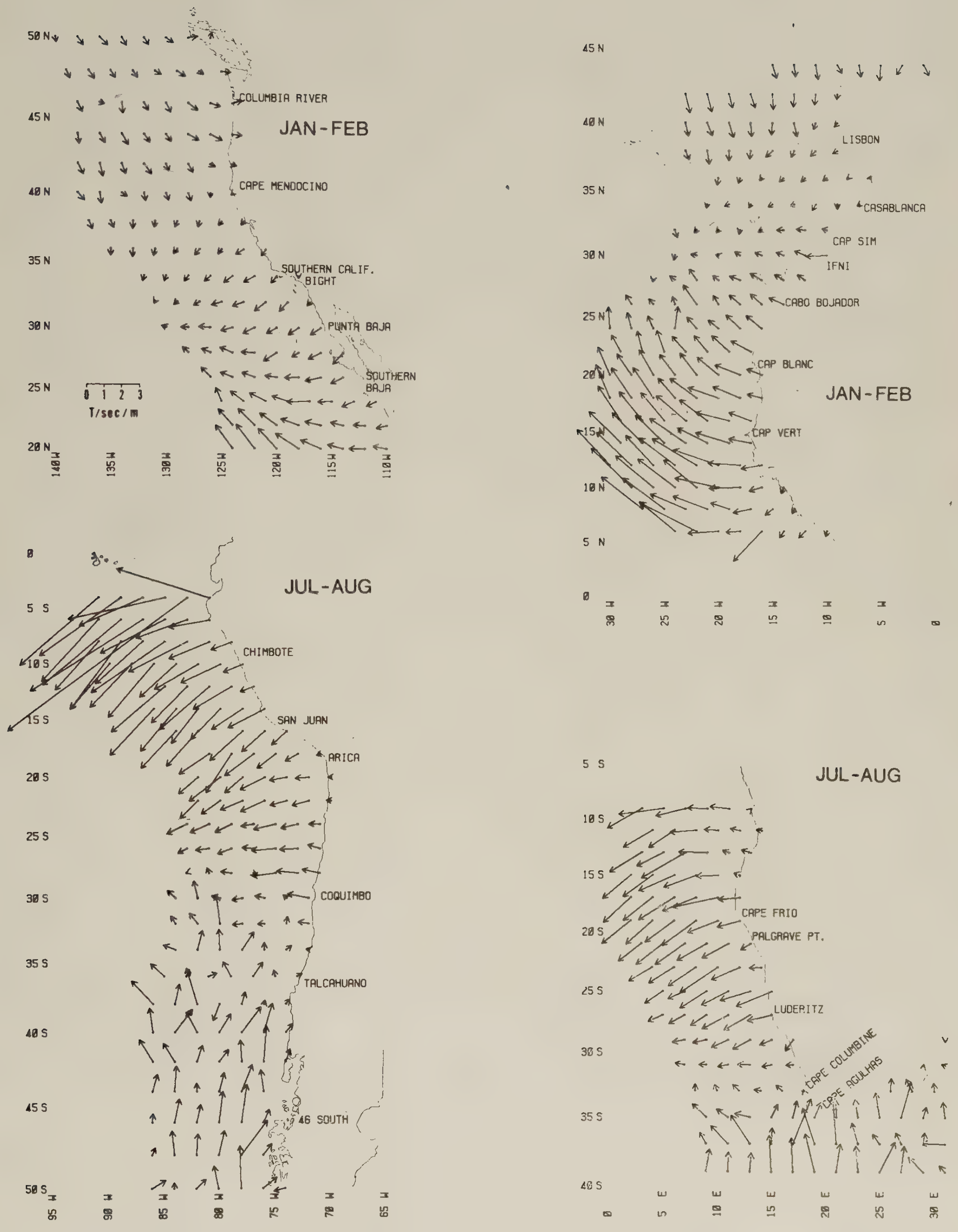

JAN-FEB
50 N
45 N
40 N
35 N
30 N
25 N
20 N
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
0 1 2 3
T/sec/m
140 W
135 W
130 W
125 W
120 W
115 W
110 W
JAN-FEB
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
30 W
25 W
20 W
15 W
10 W
5 W
0
JUL-AUG
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JUL-AUG
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 8. Winter surface Ekman transport (t sec^{-1} m^{-1})

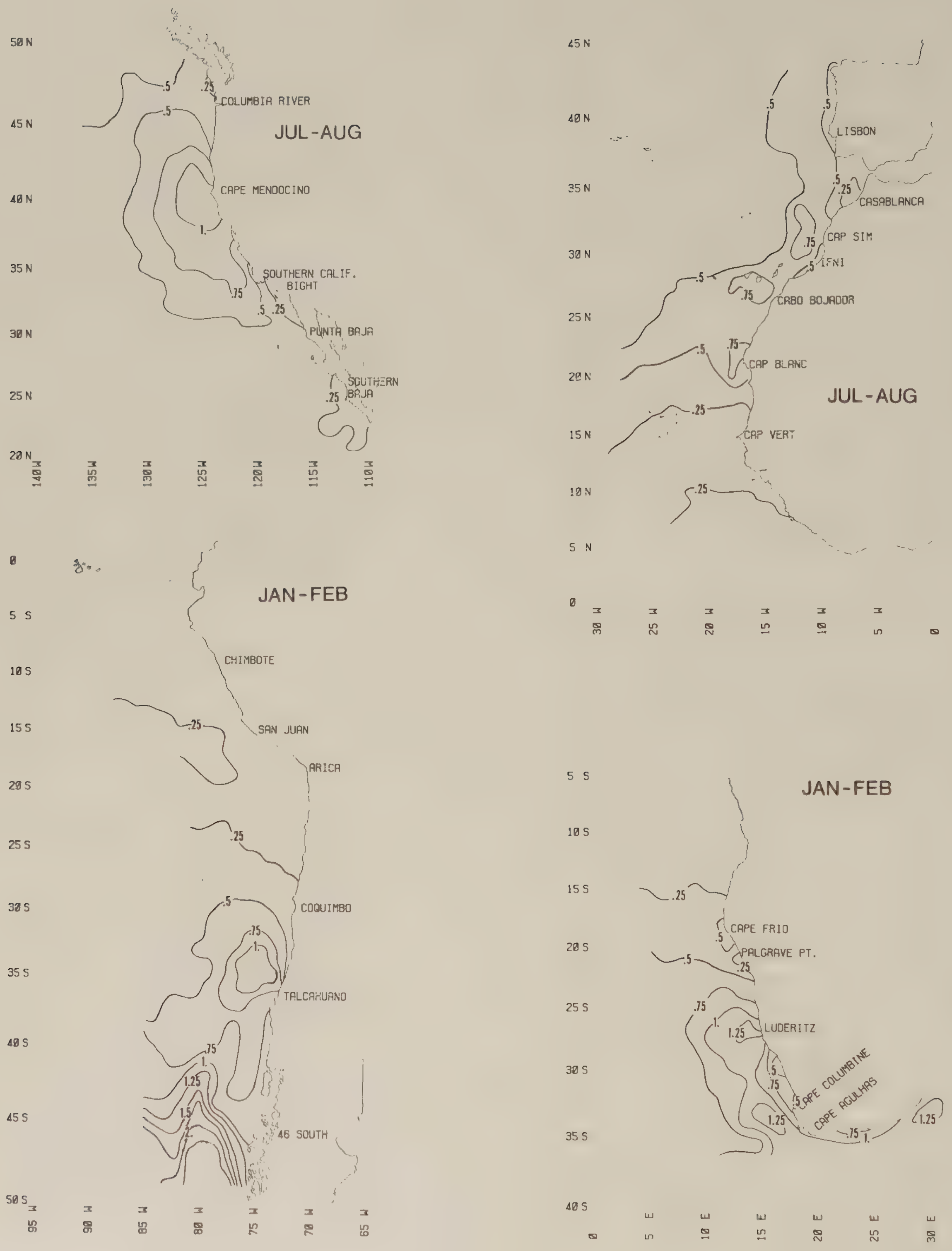

JUL-AUG
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
.5
.25
.5
1.
.75
.5
.25
.25
JUL-AUG
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
.5
.5
.5
.25
.75
.5
.5
.75
.5
.75
.25
.25
JAN-FEB
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
.25
.25
.5
.75
1.
.75
1.
1.25
1.5
2.
JAN-FEB
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
.25
.5
.5
.25
.75
1.
1.25
.5
.75
.5
1.25
.75
1.
1.25

Chart 9. Summer distributions of wind speed cubed (units of 1000 $m^3 sec^{-3}$).

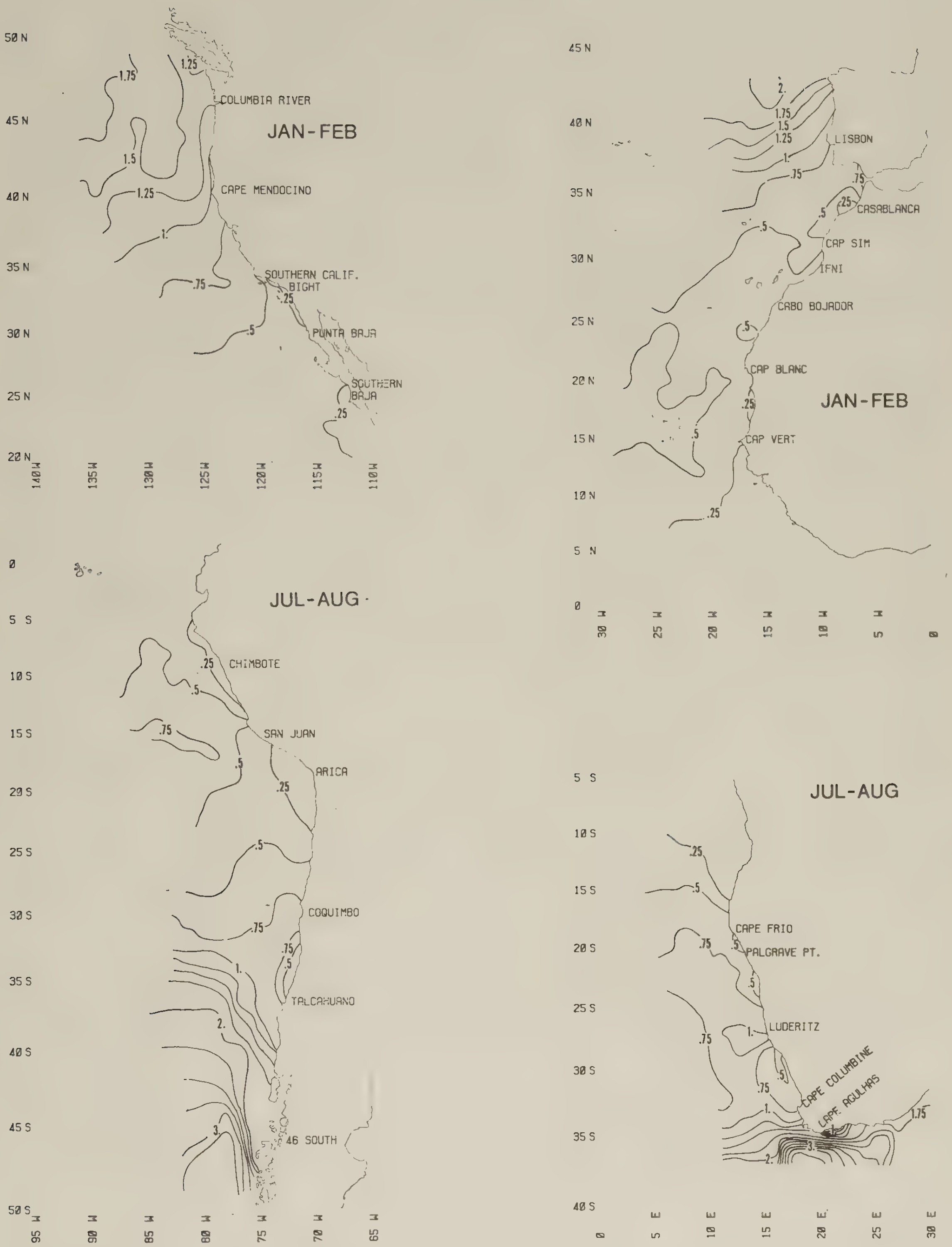

JAN-FEB
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
1.75
1.25
1.5
1.25
1.
.75
.25
.5
.25
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
JUL-AUG
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
.25
.5
.75
.5
.25
.5
.75
.75
.5
1.
2.
3.
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JAN-FEB
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
2.
1.75
1.5
1.25
1.
.75
.75
.25
.5
.5
.5
.25
.5
.25
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
JUL-AUG
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
.25
.5
.75
.5
.5
1.
.75
.5
.75
1.
2.
3.
1.75
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 10. Winter distributions of wind speed cubed (units of 1000 $m^3 sec^{-3}$).

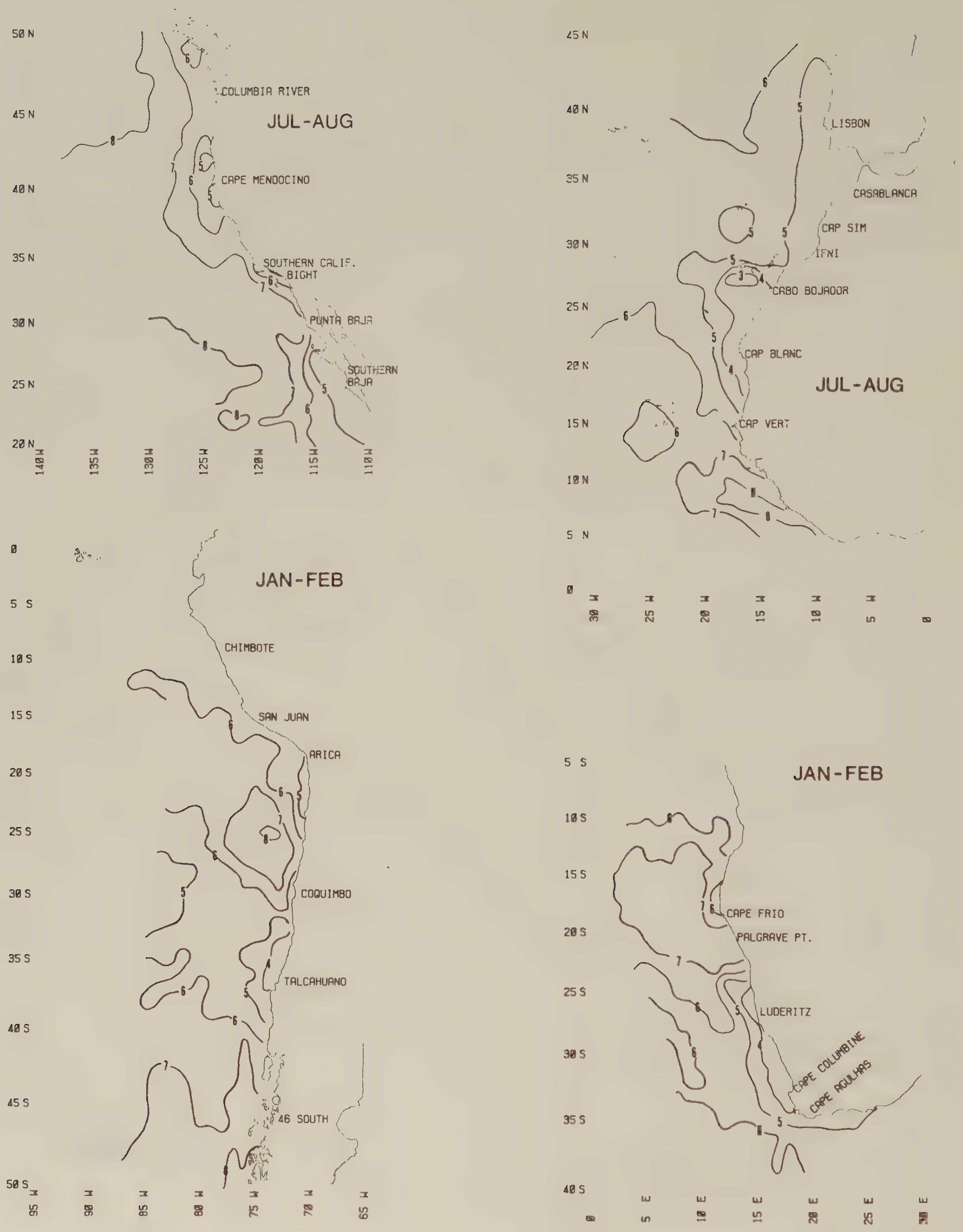

JUL-AUG
50 N
45 N
40 N
35 N
30 N
25 N
20 N
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
140 W
135 W
130 W
125 W
120 W
115 W
110 W
JUL-AUG
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
30 W
25 W
20 W
15 W
10 W
5 W
0
JAN-FEB
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
95 W
90 W
85 W
80 W
75 W
70 W
65 W
JAN-FEB
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
0
5 E
10 E
15 E
20 E
25 E
30 E

Chart 11. Summer distributions of total cloud amount (tenths of sky obscured).

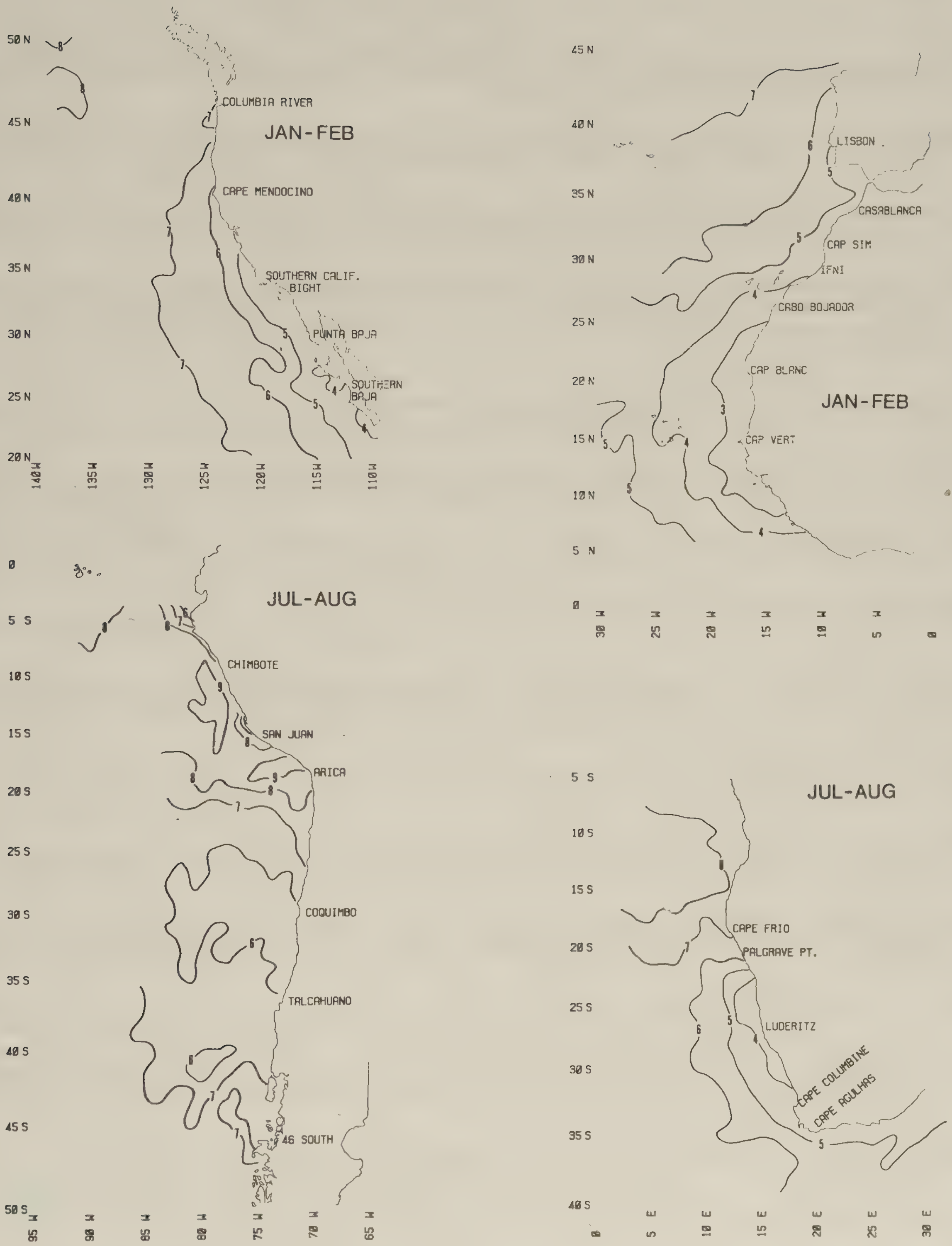

JAN-FEB
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
8
7
6
5
4
JUL-AUG
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
46 SOUTH
0
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
9
8
7
6
JAN-FEB
LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
0
7
6
5
4
3
JUL-AUG
CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
0
5 E
10 E
15 E
20 E
25 E
30 E
8
7
6
5
4

Chart 12. Winter distributions of total cloud amount (tenths of sky obscured).

REFERENCES

Ahlstrom, E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl.Serv., Fish.Bull. 60:107-146.

____________. 1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif.Coop.Oceanic Fish.Invest., Rep. 10:31-52.

Badenhorst, A. and A.J. Boyd. 1980. Distributional ecology of the larvae and juveniles of the anchovy Engraulis capensis Gilchrist in relation to the hydrological environment off South West Africa, 1978/79. Fish.Bull.S.Afr. 13:83-106.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep.Commer. NOAA Tech.Rep.NMFS SSRF-671, 103 p.

Bakun, A. and C.S. Nelson. 1977. Climatology of upwelling related processes off Baja California. Calif. Coop.Oceanic Fish.Invest.Rep. 19:107-127.

Bakun, A. and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes, Lima, Peru. 20 April-5 May 1980. IOC Workshop Rep. 28, UNESCO, Paris, p. 67-104.

____________. 1982. Turbulence, transport and pelagic fish in the California and Peru Current systems. Calif.Coop.Oceanic Fish.Invest.Rep. 23:99-112.

Bakun, A., D.R. McLain and F.V. Mayo. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish.Bull., U.S. 72(3):843-844.

Bang, N.D. and W.R.H. Andrews. 1974. Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. J.Mar.Res. 32(3):405-417.

Barkley, R.A. 1968. Oceanographic Atlas of the Pacific Ocean. Univ. of Hawaii Press, Honolulu, 20 p., 156 charts.

Belveze, H. and J. Bravo de Laguna. 1980. Les ressources halieutiques de l'atlantique centre-est. Deuxieme partie: Les ressources de la cote ouest-africaine entre 24°N et le Detroit de Gibraltar. FAO Doc.Tech.sur les peches, FIRM/T 186.2 (Fr.) 64 p.

Bernstein, R.L., L. Breaker and R. Whritner. 1977. California Current eddy formation: ship, air and satellite results. Science. 195:353-359.

Bohnecke, G. 1936. Temperatur, Salzgehalt und Dichte an der Oberflache des Atlantischen Ozeans. Atlas. "Meteor" Rep. 5. 74 charts.

Bravo de Laguna, J., M.A.R. Fernandez and J.C. Santana. 1976. The Spanish fishery on sardine (Sardina pilchardus Walb.) off West Africa. ICES CM 1977/G:13 Pelagic Fish (Southern) Committee.

Cañon, J.R. 1978. Distribución de la anchoveta (Engraulis ringens Jenyns) en el norte de Chile en relación a determinadas condiciones oceanográficas. Invest.Pesq.Inst.Fom.Pesq. Santiago, Chile. 30, 128 p. (Also available in English: J.R. Cañon, Distribution of anchoveta (Engraulis ringens Jenyns) in northern Chile in relation to selected oceanographic conditions, M.S. thesis, Oregon State University, Corvallis, 1973. 106 p.

Cram, D. 1981. Hidden elements in the development and implementation of marine resource conservation policy: The case of the South West Africa/Namibian fisheries. In Resource management and environmental uncertainty. (M.H. Glantz and J.D. Thompson, eds). John Wiley and Sons, New York. p. 137-158.

Crawford, R.J.M. 1980. Seasonal patterns in South Africa's western cape purse-seine fishery. J.Fish.Biol. 16:649-664.

Crawford, R.J.M., P.A. Shelton and L. Hutchings. 1980. Implications of availability, distribution and movements of pilchard sardinops ocellata and anchovy Engraulis capensis for assessment and management of the South African purse-seine fishery. Rapp.P.-v.Reun.Cons.int.Explor.Mer. 177:355-373.

Darbyshire, M. 1966. The surface waters near the coasts of southern Africa. Deep-Sea Res. 13(1):57-81.

Ekman, V.W. 1905. On the influence of the earth's rotation on ocean currents. Ark.Mat.Astron.Fys. 2(11):1-55.

Food and Agriculture Organization of the United Nations. 1978. Report of the ad hoc working group on sardine (Sardina pilchardus Walb.) CECAF/ECAF Series/78/7(En), 35 p.

Guillen, O. 1980. The Peru current system. I: Physical aspects. In Proceedings of the workshop on the phenomenon known as "El Nino". UNESCO, Paris:185-216. In English and Spanish.

Gunther, G.R. 1936. A report on oceanographical investigations in the Peru Coastal Current. Discovery Rep. 13:17-276.

Hart, T.J. and R.I. Currie. 1960. The Benguela Current. Discovery Rep., 31:123-298.

Hessleberg, T.H. and H.U. Sverdrup. 1915. Die Stabilitatsverhaltnisse des Seewassers bei vertikalen Verschiebungen. Bergens Museums Aarbok 1914-15. No. 15, 16 p.

Hickey, B.M. 1979. The California Current System - hypotheses and facts. Progress in Oceanography, 8(4):191-279.

Husby, D.M. and C.S. Nelson. 1982. Turbulence and vertical stability in the California Current. Calif.Coop.Oceanic Fish.Invest.Rep. 23:113-129.

Hughes, P. and E.D. Barton. 1974. Stratification and water mass structure in the upwelling area off northwest Africa in April/May 1969. Deep-Sea Res., 21:611-628.

Huyer, A. 1976. A comparison of upwelling events in two locations: Oregon and Northwest Africa.J.Mar.Res. 34(4):531-546.

Jordán, R.S. 1980. Biology of the anchoveta: I. Summary of the present knowledge. In Proceedings of the workshop on the phenomenon known as "El Niño". UNESCO, Paris: 249-278. In English and Spanish.

King, D.P.F. 1977. Distribution and relative abundance of eggs of South West African pilchard Sardinops ocellata and anchovy Engraulis capensis, 1971/72. Fish.Bull.S.Afr., 9:23-31.

Kramer, D. and J.R. Zweifel. 1970. Growth of anchovy larvae (Engraulis mordax Girard) in the laboratory as influenced by temperature. Calif.Coop.Oceanic Fish.Invest.Rep. 14:84-87.

Lafond, E.C. 1951. Processing oceanographic data. U.S. Navy Hydrographic Office, H.O.Pub. No. 614, Washington, D.C. 114 pp.

Lasker, R. 1964. An experimental study of the effects of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia, No. 2:399-405.

____________. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors leading to recruitment failure. Rapp.P.-v.Reun.Cons.int.Explor.Mer. 173:212-230.

Le Clus, F. 1979. Oocyte development and spawning frequency in the South West African pilchard Sardinops ocellata. Fish.Bull.S.Afr. 12:53-68

Levitus, S. 1982. Climatological Atlas of the World Ocean. U.S.Dep.Commer., NOAA Prof.Pap. 13. 173 p.

Levitus, S. and A.H. Oort. 1977. Global analysis of oceanographic data. Bull.Amer.Meteor.Soc. 58(12):1270-1284.

McDowell, S.B. 1962. Personal letter to A.J. Liebling. p. 189-202. In A.J. Liebling, "Onward and upward with the arts: The soul of bouillabaisse". The New Yorker, October 27, 1962.

Mittelstaedt, E. 1974. Some aspects of the circulation in the north-west African upwelling area off Cap Blanc. Tethys, 6(1-2):89-92.

Mooers, C.N.K. and J.S. Allen. 1973. Final report of the Coastal Upwelling Ecosystems Analysis Summer 1973. Theoretical Workshop. School of Oceanography, Oregon State Univ. Corvallis, Oregon. 212 p.

Nelson, C.C. 1977. Wind stress and wind stress curl over the California Current. U.S. Dep.Commer. NOAA Tech.Rep. NMFS SSRF-714, 87 p.

Nelson, C.S. and D.M. Husby. 1983. Climatology of surface heat fluxes over the California Current region. U.S.Dep.Commer. NOAA Tech.Rep. NMFS SSRF-763, 155 p.

Nelson, G. and L. Hutchings. MS. The Benguela upwelling area. Sea Fisheries Institute, Cape Town, South Africa, 32 p.

Neumann, G. and W.J. Pierson, Jr. 1966. Principles of Physical Oceanography, Prentice-Hall, Englewood Cliffs, 545 p.

Niller, P.P. and E.B. Kraus. 1977. One-dimensinal models of the upper ocean. p. 143-172. In Modelling and prediction of the upper layers of the ocean. (E.B. Kraus, ed.) Pergamon Press, New York,

Parrish, R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1(2):175-203.

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung. 28:251-282.

Pavlova, Y.V. 1966. Seasonal vartiations of the California Current. Oceanol. 6(6):806-814.

Radovich, J. 1981. The collapse of the California sardine fishery: what have we learned? p. 107-306. In Resource management and environmental uncertainy: lessons from coastal upwelling fisheries. (M.H. Glantz and J.D. Thopson, eds.) John Wiley and Sons, New York.

Rebert, J.P. 1978. Note on the hydrology of the west African continental shelf, from Mauritania to Guinea (Annex 9). p. 87-92. In Report of the ad hoc working group on West African coastal pelagic fish from Mauritania to Liberia (26°N to 5°N). CECAF/ECAF Series 78/10 (En).

Reed, R.K. and D. Halpern. 1976. Observations of the California Undercurrent off Washington and Vancouver Island. Limnol.Oceanogr. 21(3):389-398.

Reid, J.L., Jr. 1967. Oceanic environments of the genus Engraulis around the world. Calif.Coop.Oceanic Fish.Invest. Rep. 11:29-33.

Reid, J.L., Jr., G.I. Roden and J.G. Wyllie. 1958. Studies of the California Current System. Calif.Coop.Oceanic Fish.Invest., Prog.Rep., 1 July 1956 to 1 January 1958. p. 27-57.

Robles, F.L.E. 1979. Water masses and circulatiopn in the S.E. Pacific and the "El Nino" event. Ph.D. Thesis, University of Wales, Swansea, 175 p. 156 charts.

Santander, H. and O.S. de Castillo. 1979. El ictioplancton de la Costa Peruana. Bol.Inst.Mar.Peru. 4(3):69-112.

Serra, J.B., M.H. Aguayo, O.J. Rojas, F.C. Inostroza and J.C. Canon. 1979. Sardina Española. 37 p. In Estado actual de principales pesquerias nacionales. Instituto de Fomento Pesquero, Chile, Shannon, L.V. 1970. Oceanic circulation off South Africa. Fish.Bull.S.Afr. 6:27-33.

Shelton, P.A. and L. Hutchings. 1982. Transport of anchovy, Engraulis capensis Gilchrist, eggs and early larvae by a frontal jet current. J.Cons.int.Explor.Mer. 40:185-198.

Silva, S.N. and S. Neshyba. 1979. On the southernmost extension of the Peru-Chile Undercurrent. Deep-Sea Res. 26A:1387-1393.

Smith, R.L. 1978. Physical oceanography of coastal upwelling regions. A comparison: Northwest Africa, Oregon and Peru. Symposium on the Canary Current: Upwelling and Living Resources, No. 40, 10 p.

Stander, G.H. 1964. The pilchard of South West Africa. The Benguela Current off South West Africa. Investl.Rep.Mar.Res.Lab., S.W.Afr. 12, 122 p.

Stander, G.H. and A.H.B. de Decker. 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. Investl.Rep.Div.Sea Fish.S.Afr. 81:1-46.

Sverdrup, H.U. and R.H. Fleming. 1941. The waters off the coast of Southern California, March to July 1937. Bull.Scrips Inst.Oceanogr. Univ. of Calif. La Jolla. 4:261-378.

Sverdrup, H.U., M.W. Johnson and R.H. Fleming. 1942. The oceans: their physics, chemistry and general biology. Prentice-Hall, Englewood Cliffs. 1087 p.

Tomczak, M., jr. 1981. Prediction of environmental changes and the struggle of the third world for national independence: The case of the Peruvian fisheries. p. 401-438. In Resource management and environmental uncertainty. (M.H. Glantz and J.D. Thompson, eds.) John Wiley and Sons, New York.

Troadec, J.-P., W.G. Clark and J.A. Gulland. 1980. A review of some pelagic fish stocks in other areas. Rapp.P.-v.Reun.Cons.int.Explor.Mer. 177:252-277.

Wooster, W.S. and J.H. Jones. 1970. California undercurrent off northern Baja California. J.Mar.Res. 28(2):235-250.

Wooster, W.S. and J.L. Reid, Jr. 1963. Eastern boundary currents. p. 253-280. In The Sea. Vol. 2. (M.N. Hill, ed.) Interscience Publ., New York.

Wooster, W.S. and H.A. Sievers. 1970. Seasonal variations of temperature, drift, and heat exchange in surface waters off the west coast of South America. Limnol.Oceanogr. 15:595-605.

Wylie, J.G. 1966. Geostrophic flow of the California Current at the surface and at 200 m. Calif.Coop.Oceanic Fish.Invest., Atlas No. 4, XXII p, 288 charts.

Wyrtki, K. 1965. Summary of the physical oceanography of the eastern Pacific Ocean. Inst. of Mar.Res.Ref. 65-10, Scripps Inst.Oceanogr., Univ. of Calif., La Jolla. 69 p. 9 charts.

SPECIES INTERACTIONS IN THE DYNAMICS OF PLANKTIVOROUS FISH ASSEMBLAGES IN LAKE MICHIGAN

by

John J. Magnuson[1] and Larry B. Crowder[2]

[1]Center for Limnology and
Department of Zoology
University of Wisconsin
Madison, Wisconsin 53706
USA

[2]Department of Zoology
North Carolina State University
Raleigh, North Carolina 27605
USA

Resumen

Las comunidades de peces planctívoros del Lago Michigan han fluctuado grandemente tanto en la composición por especies como en abundancia. La pesquería ha variado drámaticamente durante el último siglo. Gran parte de la variabilidad ha ocurrido a través de disturbios no intencionados y manipulaciones planeadas por el hombre.

Los estudios descritos se centran en la alosa (*Alosa psuedoharangus*), eperlano arco iris (*Osmerus mordax*), y juveniles de arenque (*Coregonus hoyi*). La alosa y el eperlano arco iris son peces exóticos mientras que el arenque es una especie sobreviviente de aguas profundas del lago.

La Lamprea de Mar invadió el sistema de los Grandes Lagos en 1829 y junto con las pesquerías selectivas por tamaños, eliminaron especies de peces comerciales de tamaño grande a mediados de los años 1950s. El eperlano entró al sistema en 1912, aumentando rápidamente en el Lago Michigan a mediados de los años 1930s. La alosa invadió el sistema y aumento drámaticamente durante los años 1960s. Entre los planctívoros nativos se incluyen siete especies de *Coregonus*, de las cuales seis se han extinguido desde que el aumento de alosa comenzó.

El Lago Michigan es un sistema relativamente grande pero de baja diversidad, es también un sistema relativamente cerrado, y por lo tanto tiene una pobre amortiguación contra los cambios.

Se ha documentado la competencia entre alosa, eperlano y peces planctívoros nativos, aparentemente la fuerte competencia entre alosa y arenque ha resultado en cambios en las características del aparato alimenticio del arenque desde los años 1960s. También se han documentado cambios ecológicos, y el arenque ha desplazado a la alosa después que estos cambios ocurrieron. Se revisa la compleja evolución de estas interacciones y se considera que la competencia es una fuerza causal importante de los cambios observados en las comunidades.

Ciertamente la predación es una causa importante de los cambios inducidos por la Lamprea de Mar. También la predación de huevos por parte de los peces exóticos ha sido clave en la reducción de especies planctívoras nativas. Se discuten las fluctuaciones del reclutamiento inducidas por predación de huevos así como los posibles efectos de la reintrodución de algunas especies que han estado ausentes del Lago Michigan por algún tiempo.

Estas observaciones están relacionadas con los sistemas océanicos neríticos y sus cambios.

INTRODUCTION

Competition and predation are two species interactions that are important in the dynamics of fish assemblage structure. The planktivorous fish assemblages of Lake Michigan (North America) have fluctuated greatly both in species composition and in the abundance of individual species. Our purpose here is to evaluate the evidence for the importance of competition and predation in these dynamics. We also consider the applicability of results from Lake Michigan to other neritic systems.

The fish communities and thus the fisheries of the Laurentian Great Lakes of North America have been highly variable over the past half century. This variability has complicated the use and management of the fishery resources. Much of this variability (population extinctions, exponential growth of exotic fishes, the collapse and reopening or genesis of commercial and sport fisheries) has occurred through unintentional disturbances and planned manipulations by humans. These large-scale variations are best known in Lake Michigan (Smith 1970; Wells and McLain 1972, 1973; Christie 1974) and serve as experiments on fish community structure and species interactions in a low diversity, neritic fishery.

Our attention focuses on the three abundant pelagic planktivores-- the alewife *Alosa pseudoharengus*, the rainbow smelt *Osmerus mordax* and the young of bloaters *Coregonus hoyi*. The alewife and smelt are exotics and the bloater is a surviving species of deep water lake herring or cisco. The dynamics of these three species were greatly influenced by the interactions between the sea lamprey *Petromyzon marinus* and the primary native piscivore - lake trout *Salvelinus namaycush* (Lawrie 1970). The sea lamprey invaded the Upper Great Lakes via the Welland Canal built around Niagara Falls in 1829. Together with a size selective fishery, sea lamprey eliminated the larger commercial fishes including lake trout by the mid 1950s. Smelt was introduced into the Lake Michigan drainage in 1912 and subsequently spread throughout the Upper Great Lakes, increasing rapidly in Lake Michigan in the 1930s. Alewife invaded the Great Lakes via the Welland Canal and increased exponentially in the early 1960s, presumably due to the absence of large piscivores. Native planktivores originally included 7 native ciscoes. Six of these went extinct during the increase of alewife and rainbow smelt.

By the mid 1960s Lake Michigan was yielding little of its natural productivity to commercial or sport fisheries. In response to this problem management measures were taken to reduce sea lamprey populations with a selective toxicant for ammocetes (Lawrie 1970). Then lake trout and several non-native piscivores were restocked, beginning in 1965. The salmonid stocking program in Lake Michigan has led to a valuable sport fishery. However, natural reproduction of stocked salmonids is still relatively rare. Thus the system depends strongly on fishery management to stock piscivores and control sea lamprey.

We think that an understanding of predation and competition among the planktivores is important to fishery management decisions for Lake Michigan. The effects of these processes apparently have contributed greatly to the instability of the fisheries in Lake Michigan. In addition, the three planktivores abundant now (alewife, smelt, and bloater) provide both the forage base for the salmonid sport fishery and in the case of the bloater an important commercial fishery.

A number of characteristics of Lake Michigan make it useful for examining the importance of species interactions in neritic fisheries. First, the extent of historical manipulations and their documentation is perhaps unparalleled. Second, recent laboratory and field observations on resource use, foraging behavior and functional morphology provide clues for interpreting historical as well as contemporary data. Third, Lake Michigan while moderately large (1/10 the area of the North Sea) is a relatively closed system. This reduces colonization from other stocks of the same species or from other species with similar characteristics. Fourth, Lake Michigan is a low diversity system relative to many nearshore marine systems. These last two characteristics suggest that the Lake Michigan fish community may be more poorly buffered and less resilient to change than nearshore marine fish communities. This poor buffering may allow the effects of species interactions among planktivores in Lake Michigan to be more easily observed than in comparable marine systems.

COMPETITION

Alewife, smelt and native planktivores use the same food resources. Both native and exotic planktivores in Lake Michigan shared many prey types (Wells and Beeton,1963; Morsell and Norden,1968; Janssen and Brandt 1980; Wells 1980; Crowder et al.,1981). Also large-bodied zooplankton may have become limiting during the increase of alewife (Wells 1960, 1970). A dramatic reduction in the mean size of zooplankton at the peak of alewife abundance suggests intense planktivory and limited food resources of preferred size for planktivores. This absence of large-bodied zooplankton may have favored alewife over the native ciscoes.

Available data on the feeding behavior of alewife and the bloater support the idea that alewife is more efficient at feeding on small prey owing to ability to switch feeding modes from particulate feeding to filtering (Janssen 1976; Crowder and Binkowski 1983). But bloater appears to be more efficient than alewife when foraging on benthic prey. The zooplankton feeding stage, in bloater then becomes a "bottleneck" for recruitment of larger bloaters to the benthos. If bloaters make it through the zooplankton feeding stage, it appears that they can succeed relative to alewife in the near bottom habitat.

Alewife and smelt may compete for food. Smelt and alewife eat similar foods (Crowder et al., 1981) and smelt decreased in abundance as alewife increased in abundance in Lake Michigan (Christie,1974).

Competition for food among the species may be minimized by spatial segregation of competitors. Temperature drives physiological rates and thus has important consequences for survival and growth of fishes (Kitchell et al.,1977). In pelagic systems, temperature may provide a gradient for spatial segregation of species with similar food habits (Magnuson et al., 1979). Brandt et al. (1980) provided evidence for segregation by thermal habitat of major planktivores in Lake Michigan. Complementarity in the use of thermal habitat and food has also been demonstrated in Lake Michigan fishes (Crowder et al., 1981). Native fishes that overlap the thermal habitats of alewife and smelt use different foods. This pattern of resource subdivision often has been attributed to competition (Schoener 1974), though other interactions and environmental changes will certainly influence resource use.

Additional lines of evidence for competition between alewife and bloater deal with the habitat and diet shifts of bloater and character displacements of the feeding apparatus of bloater that occurred when alewife became abundant. During this period, young bloater shifted to a more benthic life style and had a reduction in the length and number of gill rakers (Crowder MS, b).

Prior to the increase of alewives, bloaters less than 178 mm were rarely caught in extensive bottom trawling over several years (Wells and Beeton 1963; Wells 1968). A few bloaters less than 178 mm were caught in midwater trawls and these were primarily zooplanktivorous (Wells and Beeton,1963). Small bloaters (49-145 mm) are now caught regularly on the bottom (Crowder and Magnuson,1982). Of the fishes caught in 48 tows during August 1979, 42% were bloaters, 71% of which were small-sized individuals. These small bloaters were probably young-of-year and yearlings based on their size (Edward Brown, Jr., Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Michigan). Diets of these small bloaters were dominated by benthic prey, especially the large amphipod *Pontoporeia hoyi*, (Crowder MS, a). Bloaters collected in 1979 also have significantly fewer and shorter gill rakers than those collected in 1960 by Stan Smith (Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Michigan, unpublished data) (Crowder MS, b). Both ecological and morphological data suggest an earlier shift to benthos in bloaters following the alewife invasion. These habitat, diet, and morphological changes are striking and would reduce competition with the more efficient pelagic planktivore, the alewife.

This evolving difference in life style of bloater in the face of competition with alewife for zooplankton may also explain another habitat shift we observed as bloater increased in abundance during the later 1970s (Crowder and Magnuson,1982). But in this case the bloater in the near bottom waters displaced the alewife. When we began our study of species interactions in Lake Michigan in 1977, bloaters were extremely rare. The commercial fishery for bloaters had been closed and our catch of bloaters in fall 1977 amounted to 0.3% of the total fish caught in all day bottom trawls. Alewife were abundant in all day bottom trawling and occurred at temperatures preferred in the laboratory.

We repeated the 1977 sampling in fall 1979. Between 1977 and 1979, bloater occupied the thermal habitat that had been occupied by alewife in 1977 and adult alewife near bottom at night occupied colder water (Crowder and Magnuson, 1982). Bloater appears more efficient than alewife when feeding on near bottom food resources (Crowder and Binkowski, 1983). Since total catch of alewife was not reduced in 1979, and since predation intensity by salmonids on alewife did not change drastically between 1977 and 1979 (Stewart et al. 1981), we favor the hypothesis that the altered thermal distribution of alewife resulted from competitive interactions with bloater (Crowder and Magnuson, 1982).

These later observations (i.e., bloater wins) also suggest that the interaction leading to the initial declines of native ciscoes including bloater was more complex than the simple competitive advantage of alewife. The ability to filter smaller zooplankton confers a competitive advantage on alewife when small zooplankton predominate as they did in the mid 1960s in Lake Michigan. If zooplankton are large, as they are now (Gitter, 1982) bloater young-of-year do not suffer this relative disadvantage (Crowder and Binkowski 1983). Following the reintroduction of piscivores into Lake Michigan, forage fish populations (especially alewife) were reduced and zooplankton increased in size relative to those observed at the peak of alewife abundance. It appears then that bloaters now recruit well through the zooplankton feeding stage, given reduction in alewife abundance induced by introduced piscivores - the salmonids and lake trout.

We conclude that competition has been an important interaction among Lake Michigan planktivores. Competition among adult fishes likely regulates resource use. Competition among fishes in the first year or so of life may contribute to the inverse changes in the abundances of these species - namely the declines of native ciscoes as smelt or more importantly alewife increased in abundance.

PREDATION

Predation is well documented as an important contributor to at least one species extinction in Lake Michigan. The sea lamprey played a dominant role in the extinction of lake trout (Wells and McLain, 1972, 1973). The expanding populations of exotic alewife and smelt are implicated as a cause of observed extinctions and massive population declines of many fishes in Lake Michigan. Although competition for food resources as discussed above has been the most commonly proposed mechanism for these interactions, predation on fish eggs and ichthyoplankton also has been implicated as a mechanism as well (Crowder, 1980). Predation on fish eggs and larvae by alewife and smelt should be evaluated as a possible influence on year-to-year differences in the recruitment of native fishes that still persist, such as the bloater.

We suggest that the probability that a predator-caused extinction is more probable if the predator (1) has recently increased in abundance, (2) has a large population biomass and thus a high population consumption rate, (3) has a preference for the size or taxon in question but can maintain a high abundance on alternate prey and (4) has recruitment that is relatively independent of that prey organism's abundance. These characteristics apply to the sea lamprey, and possibly to the alewife and the smelt.

The sea lamprey increased greatly in abundance after its invasion (Shetter, 1949). Its preferred prey was lake trout (Smith, 1968). As the lake trout declined in abundance, scarring from lamprey feeding activity increased on lake whitefish *Coregonus clupeaformis*, common suckers *Catostomus commersoni*, and other species (Shetter, 1949). The abundance of sea lamprey remained high as lake trout went extinct and lamprey control measure did not become effective in Lake Michigan until after the extinction of lake trout (Wells and McLain, 1972, 1973). Also the sea lamprey spawns in streams and its young live in the soft sediments as detritivores for several years, safe from any predation by lake trout. When they metamorphose to the parasitic form and return to the lake they are already predators on the lake trout. Thus the sea lamprey, as a predator on lake trout, had the characteristics to cause the observed extinction.

The alewife also increased dramatically in abundance after its invasion into Lake Michigan (Smith 1968; Wells and McLain, 1972, 1973). Although it can feed efficiently on smaller zooplankton, i.e. it has alternate prey (Janssen, 1976; Crowder and Binkowski, 1983), its feeding preference is for zooplankton forms (Brooks and Dodson, 1965; Brooks, 1968). It was during this period of maximum alewife abundance that the mean size of zooplankton was reduced (Wells 1970). Pelagic fish eggs and ichthyoplankton were similar in size to the larger crustacean zooplankton that were reduced (Crowder 1980). Could predation by alewife on pelagic fish eggs and larvae have caused the many extinctions that occurred among native planktivores at that time of maximum alewife abundance?

Some circumstantial evidence exists for the idea that predation by plantivores on pelagic fish eggs and larvae contributed to the decline of native species (Crowder 1980). Pelagic eggs and larvae should be more available than demersal ones to pelagic planktivores such as smelt and alewife. Those species with pelagic eggs and larvae should have been more affected by alewife and smelt than were species with benthic eggs or larvae. Of the 21 species common prior to the invasions, 10 or about half had pelagic eggs, based on Balon's (1975) classification of reproductive guilds. After the increase of alewife (and smelt), only two of these species remained abundant. Eight are either extinct or rare. None of those with benthic eggs or larvae went extinct. A comparison between one pair of congeners makes the difference even more clear. Emerald shiner *Notropis atherenoides* with large pelagic eggs was abundant until about 1960 in southern Lake Michigan, and had supported a minor bait fishery. It was extinct by 1963 when alewife was abundant (Smith 1970). The congener, the spottail shiner *Notropis hudsonius*, with small demersal eggs did not become extinct (Crowder 1980).

As zooplankton were reduced by alewife in the 1960s, zooplankters, longer than 1.1 mm became extremely rare (Wells 1970). The eggs and early larvae of the 10 fishes with pelagic eggs should have become rare provided alewife responded to them in the same way as they did to larger zooplankton. The diameters of these eggs ranged from 1.25 to 3.25 mm (see Crowder 1980) or the sizes on which alewife would be more likely to gulp or particulate feed than to filter feed (see Crowder MS, a). These eggs and their larvae are certainly large enough and energetically profitable enough to be selected by planktivores. Alewife in lakes eat fish eggs (Morsell and Norden 1968) and fish larvae (Kohler and Ney 1980). The fish larvae were 9 to 26 mm long. Kohler and Ney (1980) suggested that their piscivory may have contributed to the collapse of Great Lakes fishes. However, no laboratory data exist on the selection of eggs or larvae from a pool of smaller zooplankton which are several orders of magnitude more abundant.

Alewife eggs, larvae and young tend to be in waters less than 5 m deep and thus would be largely free of predation both by the deep water ciscoes that went extinct and the surviving bloater.

We think that the alewife has the characteristics to cause an extinction of fishes with pelagic eggs and larvae in Lake Michigan with predation as the mechanism. Experiments on selective feeding on eggs and larvae are needed to confirm this inference.

Smelt has some of the same characteristics but they are less well documented. Also alewife may have influenced the abundance of smelt.

The next question is whether year-to-year variations in alewife in Lake Michigan can cause year-to-year fluctuations in the recruitment of fishes with pelagic eggs and larvae. Alewife are less abundant now than in the 1960s owing to predation on them by stocked salmonids (Stewart et al. 1981). As expected, the mean size of zooplankton has increased since the time of maximum alewife abundance (Wells 1970; Gitter 1982) presumably from the lowered rate of predation by alewife on zooplankton. The abundance of adult alewife now fluctuates from year-to-year by a factor of two or so (Hatch et al. 1981) and the species composition and mean size of the zooplankton vary from year to year (Gitter 1982). Thus, there is some evidence that zooplankton are responding to fluctuations in alewife abundance. Also bloaters are again producing strong year classes and one could speculate that reduced predation on eggs and larvae have contributed to this. Hunter (1982) argued for the role of predation in the recruitment process of marine fish. And John Hunter and John Magnuson hypothesized in Fish Ecology III (Rothschild and Rooth 1982) that planktivores as selective egg and larval predators could significantly influence year-to-year variations in recruitment of fishes via predation on planktonic eggs and larvae.

The alewife and perhaps the smelt in Lake Michigan appear to meet the necessary criteria. They are abundant, vary in abundance from year to year, and feed selectively on larger zooplankton. However, there is no direct evidence that they select the eggs and larvae from a pool of more abundant but small zooplankton. The hypothesis should be tested in a pelagic ecosystem. Lake Michigan may be an ideal model for the test because species diversity of the planktivore assemblage is low, a reasonable base of biological information is availabe on the taxa involved, and few invertebrate predators are there to complicate the study.

The next event in which predation may play a role in Lake Michigan is for stocked salmonid piscivores to alter the relative abundance of the three dominant planktivores--the alewife, smelt and bloater (Stewart et al. 1981). Stocking rates of salmonid are regulated by fishery management and may not track changes in the abundance of alewife, their dominant prey. Major time lags occur between a decision to stock and when the impact on the forage base occurs (Stewart et al. 1981). This "predator inertia" is at least 3 years for coho *Oncorhynchus kisutch* and chinook *O. tshawytscha* salmon and 5 or 6 years for lake trout (Stewart et al. 1981). Since alewife abundance has peaked about every 4 years during the late 1960s and early 1970s, salmonid stocking cannot be used as a tool to moderate these short-term variations. The problem is further complicated because of time lags involved in the assessment of alewife populations. Stocking rates therefore are set for some average condition and the potential for a mismatch between the abundance of salmonids and their prey, the alewife, is quite high in some years. Year class failures of the alewife and a shift of the salmonids to alternate prey are the expected consequences.

Our conclusions about the influence of predation on the dynamics of the assemblage of planktivores in Lake Michigan are not as firm as were our conclusions about competition. This is surprising to us since the influence of predation has generally been believed to be easier to demonstrate than the effects of competition (Connell 1975; MacLean and Magnuson 1977; Sale 1979). We do conclude that predation on pelagic eggs and larvae by alewife and smelt is implicated as a cause of extinction of fishes with pelagic eggs and larvae. Predation also may contribute to year-to-year variation in the recruitment of the surviving native planktivores such as the bloater. Predation on alewife by stocked salmonids should decrease any influence of alewife on fishes with planktonic eggs and larvae but also may cause occasional year class failures in the alewife.

APPLICABILITY TO LARGER NERITIC ECOSYSTEMS

Lake Michigan is large enough for researchers to feel that the scales on which they are working are oceanic. Yet, the role of scale on the effects of predation and competition in small isolated lakes, the Great Lakes of Africa and North America, and the expanse of the world's major seas and oceans, is poorly known. If the species interactions (competition and predation) among pelagic planktivores in lakes are greatly influenced by the "island" nature of lakes, how are the interactions of pelagic planktivores in ocean systems influenced by the "continental" nature of oceans? On what dimensions should the gradients among these aquatic environments be scaled to account for any differences in the effects of competition and predation?

In Lake Michigan the assemblage of pelagic planktivores excluding ichthyoplankton differs from larger neritic systems in at least two ways important to this paper. First, Lake Michigan is more closed to immigration species (3 planktivores at present in Lake Michigan) and is lower than our perception of species richness for many oceanic systems.

The closed or "island"-like nature of lakes is linked to their sensitivity to the invasion of predators that evolved in other systems (Magnuson 1976). The sea lamprey, the alewife, and the smelt are examples from Lake Michigan. Also in a more closed system interactions with new species are more likely to continue to extinction and to an altered community structure (both taxonomically and functionally). We expect this because immigration of new taxa or individuals is less likely to perturb the processes in a closed system than in a more open system. In an open system, recolonization could follow more closely a local extinction than in a closed system.

Species richness or diversity has often been associated with ecosystem stability in the ecological literature. Certainly in a more species-rich system, substitutions by similar species would be more probable than in a system with only a few species. Thus, the consequences of fluctuations in the abundance of a species may be greater in a species-poor system than in a species-rich system.

Among pelagic planktivores excluding ichthyoplankton, our perception is that ocean systems may be more diverse and are certainly more open than lake systems. We think these factors should have some influence on the effects of species interactions on the dynamics of these fish assemblages. More importantly, these factors plus the smaller size of Lake Michigan may make it easier to observe the effects of species interactions in Lake Michigan than in marine systems. This does not preclude the importance of these interactions in marine systems but suggests that Lake Michigan may be a useful model for observing the potential effects of predation and competition in neritic marine systems.

ACKNOWLEDGEMENTS

We thank T. Frost, C. Paszkowski and W. Tonn for critically reviewing an earlier draft.

REFERENCES

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. J.Fish.Res.Board Can. 32:821-864.

Brandt, S.B., J.J. Magnuson and L.B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Can.J.Fish.Aquat.Sci. 37:1557-1564.

Brooks, J.L. 1968. The effects of prey size selection by lake planktivores. Syst.Zool. 17:273-291.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and the composition of plankton. Science. 150:28-35.

Connell, J.H. 1975. Some mechanisms producing structured natural communities: a model and evidence from field experiments. In Ecology and Evolution of Communities. (M.L. Cody and J.M. Diamond, eds). Belknap Press, Harvard University Press, Cambridge, Massachusetts.

Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Env.Biol.Fish. 5:225-533.

____________. MSa. Optimal foraging and feeding mode shifts in fishes.

____________. MSb. Competition and character displacement in a native cisco in Lake Michigan: morphological and ecological evidence.

Crowder, L.B. and F.P. Binkowski. 1983. Foraging behaviors and the interaction of alewife (Alosa pseudoharengus) and bloater (Coregonus hoyi). Envir.Biol.Fish. In press.

Crowder, L.B. and J.J. Magnuson. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. Can.J.Fish.Aquat.Sci. 39:1046.

Crowder, L.B., J.J. Magnuson and S.B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can.J.Fish.Aquat.Sci. 38:662-668.

Christie, W.J. 1974. Changes in fish species composition of the Great Lakes, J.Fish.Res.Board Can. 31:827-854.

Gitter, M.J. 1982. Thermal distribution and community structure of Lake Michigan zooplankton with emphasis on the interactions of young-of-year fishes. MS Thesis. (Oceanography and Limnology) University of Wisconsin, Madison.

Hatch, R.W., P.M. Haack and E.H. Brown, Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967-1978. Trans.Am.Fish.Soc. 110:575-584.

Hunter, J.R. 1982. Predation and recruitment. In Fish Ecology III - A Foundation for REX Recruitment Experiment (B.J. Rothschild and C.G.H. Rooth, eds). University of Miami Technical Report 82008

Janssen, J. 1976. Feeding modes and prey size selection in the alewife (Alosa pseudoharengus). J.Fish.Res.Board Can. 33:1972-1975.

Janssen, J. and S.B. Brandt. 1980. Feeding ecology and vertical migration of adult alewife (Alosa pseudoharengus) in Lake Michigan. Can.J.Fish.Aquat.Sci. 37:177-184.

Kitchell, J.F., D.J. Steward and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). J.Fish.Res.Board Can. 34:1922-1935.

Kohler, C.C. and J.J. Ney. 1980. Piscivority in a land-locked alewife (Alosa pseudoharengus) population. Can.J.Fish.Aquat.Sci. 37:1314-1317.

Lawrie, A.H. 1970. The sea lamprey in the Great Lakes. Trans.Am.Fish.Soc. 99:766-775.

MacLean, J.H. and J.J. Magnuson. 1977. Inferences on species interactions in percid communities. J.Fish.Res.Board Can. 34:1941-1945.

Magnuson, J.J. 1976. Managing with exotics - a game of chance. Trans.Am.Fish.Soc. 105(1):1-9.

Magnusson, J.J., L.B. Crowder and P.A. Medvick. 1979. Temperature as an ecological resource. Am.Zool.. 19:331-343.

Morsell, J.W. and C.R. Norden. 1968. Food habits of the alewife, Alosa pseudoharengus, in Lake Michigan. Proc.Conf.Great Lakes Res. 11:96-102.

Rothschild, B.J. and C.G.H. Rooth. 1982. Fish Ecology III - A Foundation for REX a Recruitment Experiment. University of Miami Technical Report 82008.

Sale, P. 1979. Habitat partitioning and competition in fish communities. In Predator-Prey Systems in Fisheries Management (H. Clepper, ed.). Sport Fishing Institute of Washington, D.C.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science. 185:27-39.

Shetter, D.S. 1949. A brief history of the sea lamprey problem in Michigan waters. Trans.Am.Fish.Soc. 76:160-176.

Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. J.Fish.Res.Board Can. 25:667-693.

____________. 1970. Species interactions of the alewife in the Great Lakes. Trans.Am.Fish.Soc. 99:754-765.

Stewart, D.J., J.F. Kitchell and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans.Am.Fish.Soc. 110:751-763.

Wells, L. 1960. Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. U.S.Fish and Wildl.Serv.Fish.Bull. 60:343-369.

____________. 1968. Seasonal depth distribution of fish in southern Lake Michigan. Fish.Bull. U.S. 67:1-15.

____________. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol.Oceanogr. 14:556-565.

____________. 1980. Food of alewives, yellow perch, spottail shiners, trout-perch and slimy and fourhorn sculpins in southeastern Lake Michigan. U.S.Fish and Wildl.Serv.Tech. Papers 98.

Wells, L. and A.M. Beeton. 1963. Food of the bloater, Coregonus hoyi, in Lake Michigan. Trans.Am.Fish.Soc. 92:245-255.

Wells, L. and A.L. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. J.Fish.Res.Board Can. 29:889-898.

____________. 1973. Lake Michigan: man's effects on nature fish stocks and other biota. Great Lakes Fish.Comm.Tech.Rep.No. 20.

LOCAL STUDIES - ESTUDIOS LOCALES

POPULATION DYNAMICS AND FACTORS AFFECTING THE ABUNDANCE OF CAPELIN (*Mallotus villosus*) IN THE NORTHWEST ATLANTIC

by

J.E. Carscadden

Fisheries Research Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, Newfoundland A1C 5X1
Canada

Resumen

El Capelin (*Mallotus villosus*) es una especie pequeña que forma cardúmenes y es abundante en el Atlántico Noreste en el área de Newfoundland. Es una especie importante como especie forrajera. Hay cinco stocks de capelin en el área, aun cuando algunos de ellos pueden en realidad ser stocks complejos. A excepción de un área principal de desove ubicada mar afuera, todo el capelin desova en la playa o muy cercana a élla. La población madura se compone principalmente de individuos de tres a cuatro años de edad y la mayor parte mueren después del desove.

Durante décadas el capelin ha sido explotado por una pequeña pesquería dómestica (25 000 ton.), pero durante los años 1970s esta especie fue fuertemente explotada por una pesquería internacional mar afuera. Las capturas totales de capelin llegaron a su máximo a mediados de los años 1970s con 360 000 toneladas y después de eso han declinado. En estos momentos no hay ninguna pesquería mar afuera pero la pesquería costera ha aumentado en los últimos años debido a la demanda de huevas de capelin en el mercado Japonés.

Las evaluaciones del capelin se han hecho usando modelos de producción, técnicas acústicas y modelos para seguir la secuencia de la abundancia de capelin. Solo el último método ha proporcionado una perspectiva histórica de la dinámica de población de capelin. Estos modelos indican que la abundancia llegó a su máximo a mediados de los años 1970s, mayormente debido a la fuerte clase anual de 1973. Las clases anuales de 1974 y 1978 fueron débiles y la población declinó. Sin embargo la clase anual de 1979 parece haber sido fuerte dando como resultado que la biomasa desovante de capelin en el año 1982 fuera grande.

Las capturas fueron relativamente altas durante los años en que se produjeron pobres clases anuales, y esto tiende a implicar a la pesquería en la disminución de la población de capelin. Sin embargo, a excepción de uno de los s stocks desovantes, no se ha mostrado que la pesquería haya tenido ningún efecto mortífero en la dinámica del capelin. Las variables ambientales durante la primera etapa de la vida de capelin afectan la sobrevivencia, el crecimiento y posiblemente el reclutamiento. La mortalidad de huevos en las arenas de la playa es afectada por la temperatura de incubación, la que en difinitiva es afectada por un complejo de factores incluyendo la densidad de huevos, la temperatura del mar, temperatura máxima y mínima del aire, horas de luz, lluvia y amplitud de mareas. Estos factores varían solo ligeramente en la mayoría de las principales áreas de desove al este de Newfoundland y al sur del Labrador, y tales cambios sincronizados pueden contribuir a la fluctuación anual de las fuerzas de las clases anuales de capelin. El oleaje que es inducido por el viento que se dirige hacia la playa, es importante para facilitar la liberación de las larvas de la arena de la playa. Estos vientos hacia la playa también inducen el remplazamiento de las masas de agua de tal forma que las larvas son liberadas en aguas más cálidas, con una superficie rica en posibles presas, la cual ha remplazado aguas frías, que son ricas en predatores. Solamente se dispone de datos de dos años, 1978 y 1979, pero en esos años la densidad de huevos en la arena era aproximadamente igual. La frecuencia de vientos hacia la playa durante el período de eclosión fue 50% mayor en 1979, y la densidad de larvas en el ambiente cercano a la orilla fue 60% mayor. La biomasa desovante de capelin fue aproximadamente igual en 1978 y 1979 pero la clase anual de 1979 aparentemente es mucho mayor que la de clase anual de 1978. Análisis preliminares sugieren que hay una relación positiva entre el reclutamiento y la temperatura de la superficie del mar (0-20 m) durante las etapas tempranas de la existencia pelagíca.

De las observaciones cualitativas parece que hay dos especies cuya abundancia ha aumentado durante los períodos de baja abundancia de capelin, estos son la amodita (*Ammodytes dubius*) en el sur, y el bacalao del ártico (*Boreogadus saida*) en norte. Los estudios realizados sobre los efectos de las fluctuaciones de capelin y dos predatores principales, el bacalao (*Gadus morhua*) y el salmón (*Salmo salar*) no han llegado a establecer ninguna relación firme entre estas especies. Sin embargo, los autores de estos estudios fueron críticos de su trabajo mayormente debido a que los datos disponibles no fueron colectados para probar las relaciones que se habían postulado, o porque no dispuso de datos adecuados.

INTRODUCTION

It is probable that capelin, *Mallotus villosus*, is one of the most important fish species in the northwest Atlantic because of its position as a forage species (Bailey et al., 1974; Winters and Carscadden, 1978) and its commercial importance. This position as an important forage and commercial species has created controversy over the years; for instance, as early as 1835 fishermen complained that the "hauling of capelin for manure had proved very prejudicial to the success of the cod fishery" (Journal of the Newfoundland House of Assembly 1835). In the last decade, capelin has generated a great deal of interest both from the general public and the scientific community. This interest arose largely because of a large commercial capelin fishery that developed in the early 1970's and the potential impact of this fishery on the capelin stocks themselves and on predator stocks, many of which are commercially important.

It is the purpose of this paper to review some aspects of capelin biology, the history of the commercial fishery and its management, the population dynamics of capelin, the factors affecting the abundance of capelin, and the possible consequences of fluctuations of capelin on competitors and predators in the Newfoundland area of the northwest Atlantic.

Life History

Capelin (or caplin) are small, silvery fish closely related to smelt. They are a cold water, pelagic, schooling species inhabiting Arctic and sub-Arctic seas in the Atlantic and Pacific oceans. In the eastern Atlantic, capelin occur from western Norway to northern Russia and are widely distributed throughout the Barents Sea. They are also abundant around Iceland and Greenland. On the east coast of North America, capelin occur from Hudson Bay to Nova Scotia, but are most abundant around Newfoundland and Labrador. In the Pacific, capelin occur from Alaska to Juan de Fuca Strait and from the Sea of Chukotsk to Japan and Korea (Jangaard, 1974).

The relative distribution of capelin in the Newfoundland coastal zone varies seasonally but undoubtedly peaks in June and July, when beach spawning occurs. At other times of the year, capelin can be found in large concentrations in the offshore waters. While the distribution of young capelin is not well defined, the distribution and migration patterns of adults are better known and spawning stocks of capelin have been identified. There are five major stocks in the Newfoundland area; Labrador-northeast Newfoundland stock, NAFO* Div. 2J3K, (A); northern Grand Bank-Avalon stock, NAFO Div. 3L, (B); South Grand Bank (Southeast Shoal) stock, NAFO Div. 3NO, (C); St. Pierre-Green Bank stock, NAFO Div. 3Ps, (D); Gulf of St. Lawrence stock, (E) (Fig. 1). Some of these major stocks (eg. Labrador-northeast Newfoundland and Gulf of St. Lawrence) may be composed of a number of sub-stocks (Winters, 1974a; Sharp et al., 1978). These stocks have been identified through the knowledge of seasonal distribution patterns and growth differences (Campbell and Winters, 1973; Winters, 1974b), neristic (Sharp et al., 1978; Carscadden and Misra, 1980) and morphometric (Sharp et al., 1978) characters and the fishing patterns of the commercial capelin fleet. Besides these offshore stocks of capelin that migrate to the inshore areas or Southeast Shoal to spawn, there is also evidence to suggest that there are local stocks, probably relatively low in abundance. Like most species of fish, there is some degree of stock overlap during some part of the life cycle. Since most of the commercial fishery occurred on only three of the stocks (Div. 2J3K, Div. 3L, and Div. 3NO stocks), most of the subsequent discussion will be restricted to capelin occurring in these areas.

---

* Northwest Atlantic Fisheries Organization (formerly ICNAF, the International Commission for Northwest Atlantic Fisheries

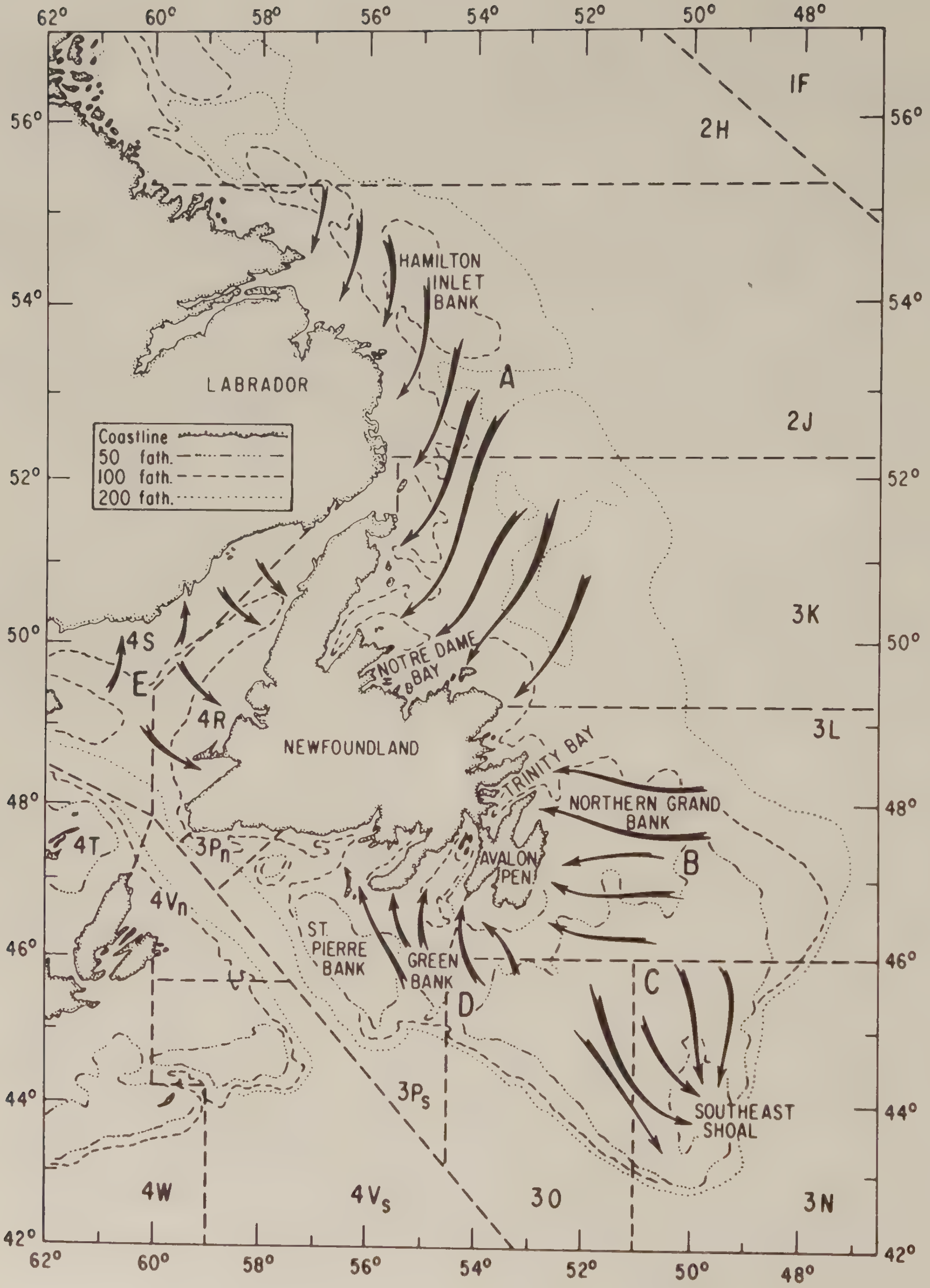

62°
60°
58°
56°
54°
52°
50°
48°
56°
54°
52°
50°
48°
46°
44°
42°
IF
2H
2J
3K
3L
3N
3O
3Ps
3Pn
4S
4R
4T
4Vn
4Vs
4W
A
B
C
D
E
HAMILTON INLET BANK
LABRADOR
NEWFOUNDLAND
NOTRE DAME BAY
TRINITY BAY
NORTHERN GRAND BANK
AVALON PEN.
ST. PIERRE BANK
GREEN BANK
SOUTHEAST SHOAL
Coastline
50 fath.
100 fath.
200 fath.

Fig. 1. Map showing major stocks and migration routes of mature capelin. Alpha-numeric designation (e.g. 2H, 2J, 3K, etc.) are NAFO Divisions.

A. Labrador - Northeast Newfoundland (NAFO Div. 2J3K) stock
B. Northern Grand Bank - Avalon (NAFO Div. 3L) stock
C. South Grand Bank (Southeast Shoal - NAFO Div. 3NO) stock
D. St Pierre - Green Bank (NAFO Div. 3Ps) stock
E. Gulf of St. Lawrence stock

The Notre Dame Bay area is known to be an over-wintering area for part of the Labrador-northeast Newfoundland stock. It seems probable that capelin also over-winter in parts of NAFO Subarea 2; maturing capelin have been taken in research catches late in the year in this area and there is no known northward migration in the spring from Div. 3K to the inshore spawning grounds in Subarea 2. During June and July, mature capelin move inshore to spawn on beaches in northeastern Newfoundland and Labrador. After spawning, most fish die. The few spawning survivors move offshore in the late summer and join immature fish to form feeding schools. Feeding is heavy from August to November and schools are found in offshore waters from Labrador to northeast Newfoundland.

The northern Grand Bank-Avalon and Southeast Shoal stocks appear to mix and over-winter on the northern part of the Grand Bank (Campbell and Winters, 1973; Carscadden and Misra, 1980). During late winter and early spring the fish become active, form feeding schools, and begin a migration to the spawning grounds. The northern Grand Bank-Avalon stock moves inshore to spawn on Newfoundland beaches while the Southeast Shoal stock moves south over the grand Bank to spawn on sandy substrate on the Southeast Shoal. Spawning in both areas occurs during June and July and post-spawning mortality is high at this time. Spawning survivors are believed to move to the northern Grand Bank area for feeding and over-wintering.

There are differences in the timing of spawning in different areas. Spawning on the west and south coasts of Newfoundland usually begins in late May. Spawning time usually becomes later further to the north such that spawning in Labrador may not occur until August in some years (Templeman, 1948). Spawning on the Southeast Shoal, the only known offshore spawning area for capelin, occurs in June and July.

The general environmental conditions present during spawning have been characterized. Capelin spawning inshore in Newfoundland and Labrador prefer water temperatures of 5.5°C-8.5°C and pebbles ranging in size from 0.5-2.5 cm in diameter (Templeman, 1948). Spawning normally occurs at night or on dull cloudy days, although there are exceptions. On the Southeast Shoal, spawning occurs in a water depth of approximately 50 m where bottom temperatures are 2-4°C (Pitt, 1958a).

Inshore spawning normally occurs for 4-6 weeks; most spawning occurs on the beaches but if water temperatures on the beach become too high, the fish will spawn in deeper water adjacent to the beaches. The extent of deepwater (non-beach) spawning is probably very variable from year to year and other factors besides water temperature on the beach may exert an influence.

Capelin mature at three or four years of age with faster growing fish maturing earlier (Winters, 1974b). In the spawning populations, three- and four-year-olds usually predominate, although other ages, including two, five, six, and seven do occur in varying proportions. As already noted, spawning mortality is high, usually being greater than 80% (Carscadden and Miller, 1980).

There is no doubt that capelin are important as a forage fish in the Newfoundland area. Perhaps the most extensively studied capelin predator is cod and there are a number of studies (see Akenhead _et al._, 1982; Lilly, 1981; Lilly _et al._, 1981 for reviews) that substantiate the observation that cod consume capelin. The broad seasonal patterns of cod predation on capelin in Div. 2J3KL and Div. 3NO have been described but in spite of the numerous feeding studies, "there is no estimate, based on adequate seasonal and spatial sampling of the contribution of capelin to the total food consumption of a single cod stock in a given year" (Lilly _et al._, 1981). However, several studies have estimated that for the Newfoundland area in general, capelin comprise about 30% of the cod's diet (Akenhead _et al._, 1982).

Although cod is the capelin predator that usually evokes the most concern, other marine species feed heavily on capelin as well. Capelin accounts for 45-100% of the food of adult salmon, depending on size, in Newfoundland coastal waters (Lear, 1972). Greenland halibut in the length range of 20-80 cm feed heavily on capelin (Lear, 1969) and American plaice (20-49 cm) in Div. 3L depend on capelin for 14-38% of their food (Pitt, 1973). Haddock, yellowtail flounder, winter flounder, skates, sea ravens, and a variety of other demersal species consume large quantities of capelin eggs and capelin during the spawning season (Pitt, 1958b; Templeman, 1968).

Marine mammals also feed heavily on capelin. Capelin are an important food for whales, including fin whales (Mitchell, 1975), minke whales, sei whales (Sergeant, 1963) and humpback whales (Lien, 1980), in the Newfoundland area. Sergeant (1973) has estimated that at least 25% of the diet of harp seals is capelin and other less abundant species of seals such as hooded, grey and harbour seals, also consume significant quantities of capelin.

Seabirds are also capelin predators; murres (Tuck, 1960), greater shearwaters, puffins, gannets, kittiwakes (Winters and Carscadden, 1978), and gulls (Lewis, 1937) all feed on capelin.

THE FISHERY AND ITS MANAGEMENT

It is only in the last decade that man has become a significant predator of capelin although capelin have been taken during the spawning season for decades. It has been estimated that prior to the 1950's 20,000-25,000 tons of capelin were taken annually in Newfoundland for bait and fertilizer and to a lesser extent for food for dog teams (Templeman, 1968; Barnes, 1974). However, with the decline in the use of dog teams and fertilizer for gardens and less demand for capelin as bait, inshore landings declined considerably. During the 1970's, interest in capelin as a commercial species increased with effort being concentrated in the offshore area in the early and mid 1970's and in the inshore area in the late 1970's.

In 1972, the first substantial offshore catches of about 70,000 tons of capelin were reported. These catches increased rapidly, peaking in 1976 at about 370,000 tons and declining since then. The catches were taken at different times of the year in different areas and details of the catches by areas (Div. 3L, Div. 3NO, and Div. 2J3K) are given in Fig. 2, 3 and 4.

The annual offshore capelin fishery normally began in March or April on fish, most of which were maturing and feeding, on the northern Grand Banks (Div. 3L). Thus, fish from two stocks, the northern Grand Bank-Avalon stock and the Southeast Shoal stock, were fished by a fleet dominated by USSR midwater trawlers. The fishing fleet followed the capelin as they moved to their spawning grounds; however, once the inshore spawning component entered Canadian territorial waters, the fleet followed the Southeast Shoal (Div. 3NO) capelin to their spawning grounds where the fishery on spawning capelin continued into July. Most of the vessels operating on the Southeast Shoal were USSR midwater trawlers and Norwegian purse-seiners.

The fishery in Div. 3L developed very rapidly with the peak catch reported in 1974, followed by a gradual decline from 1975-80 (Fig. 2). It should be noted that in 1975, Canadian ports were closed to the USSR fishing fleet because Canadian authorities accused the Soviets of taking approximately double their quota in Div. 3L. If true, the catch in 1975 (Fig. 2) should be approximately 60,000 tons. In addition, the "inshore" catch in 1974 is shown at approximately 8,000 tons, higher than the preceding and following years. This may be an anomaly caused by the grouping of the data; in the present grouping, Canadian catches were assumed to have been taken inshore since Canada has no fleet of large vessels fishing capelin. However in 1974, some catches were reported from large (500-999 GRT) purse-seiners chartered by Canadian companies. Thus, the catches may have been taken offshore and the inshore catch estimates for 1974 may be over-estimated and the offshore catch estimates under-estimated. It should also be noted that each year some unknown fraction of the Div. 3L offshore catch may have been fish from the Southeast Shoal stock. In general, the trend of catches for Div. 3L since 1974 has been a decrease in the offshore portion (offshore fishery closed in 1979) and an increase in the inshore portion. The inshore catch consists of mature capelin and has been taken entirely by Newfoundland fishermen who are attempting to satisfy the Japanese market for roe capelin.

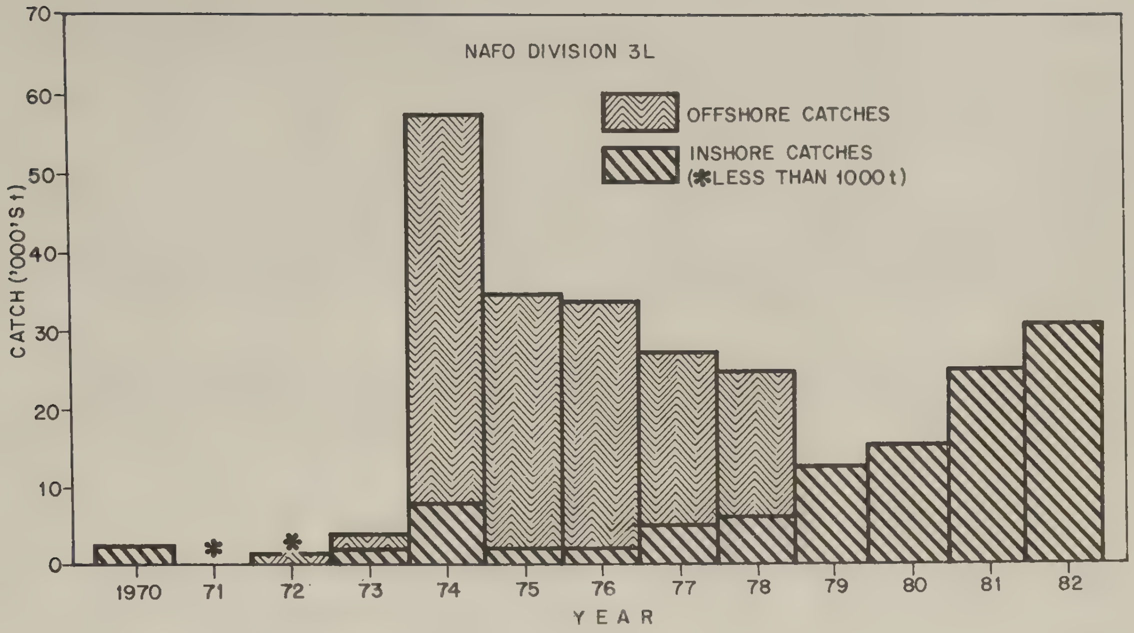
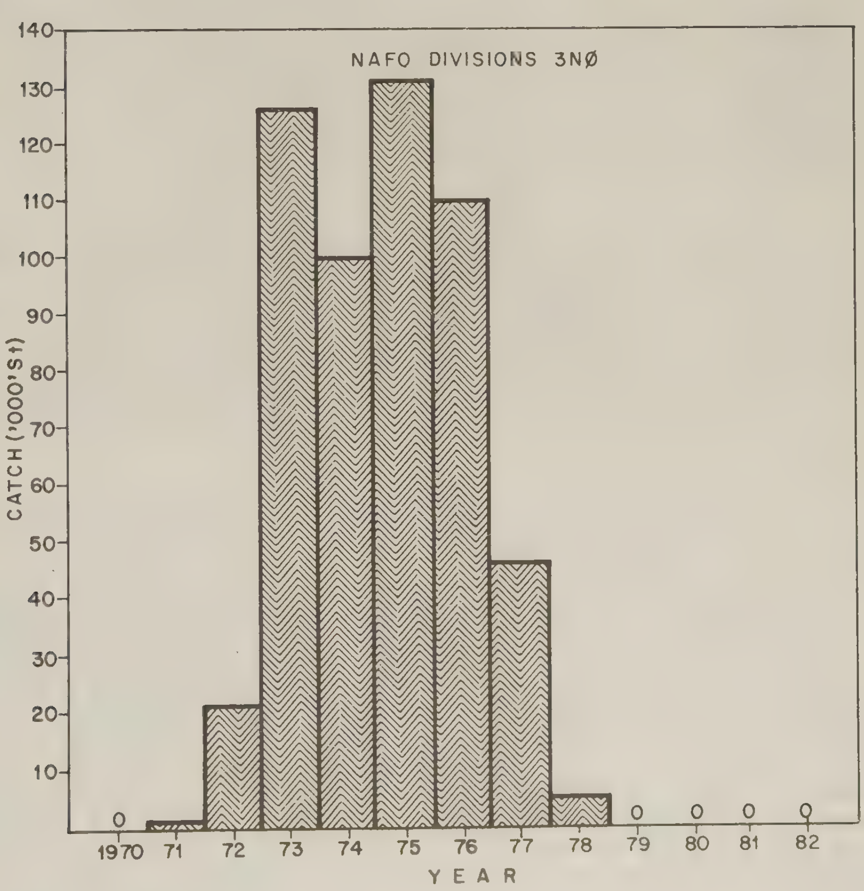


Fig. 2. Nominal catches of capelin in NAFO Div. 3L, 1970-82.
1982 catch data are preliminary.

Fig. 3. Nominal catches of capelin in NAFO Div. 3NO, 1970-82.



The catches (Fig. 3) of the Southeast Shoal stock (Div. 3NO) rose rapidly from about 21,000 tons in 1972 to a level of about 100,000 to 132,000 tons for four years between 1973-1976 and dropped quickly to 47,000 tons in 1977 and 5,000 tons in 1978. The fishery was closed in 1979 and has remained closed since then. It was the conclusion of scientists that "the intense commercial fishery on the spawning grounds in Div. 3N may have substantially reduced the spawning stock size in recent years, and the possibility of recruitment overfishing should be taken into account" (Anon., 1979).

Each year when the fishery on the Southeast Shoal stopped with the cessation of capelin spawning, the attention of the fleet shifted to Div. 2J and Div. 3K in late August or early September. This fishery, which caught feeding capelin most of which would mature and spawn the following year, was prosecruted mainly by USSR midwater trawlers and continued until November or December.

The first large catch in the Div. 2J3K capelin fishery was reported in 1972 at 46,000 tons. Catches peaked in 1976 at about 216,000 tons and declined after that to about 5,000 tons in 1980. During the period 1970-1980, inshore catches remained at a low level below 2,500 tons (Fig. 4).

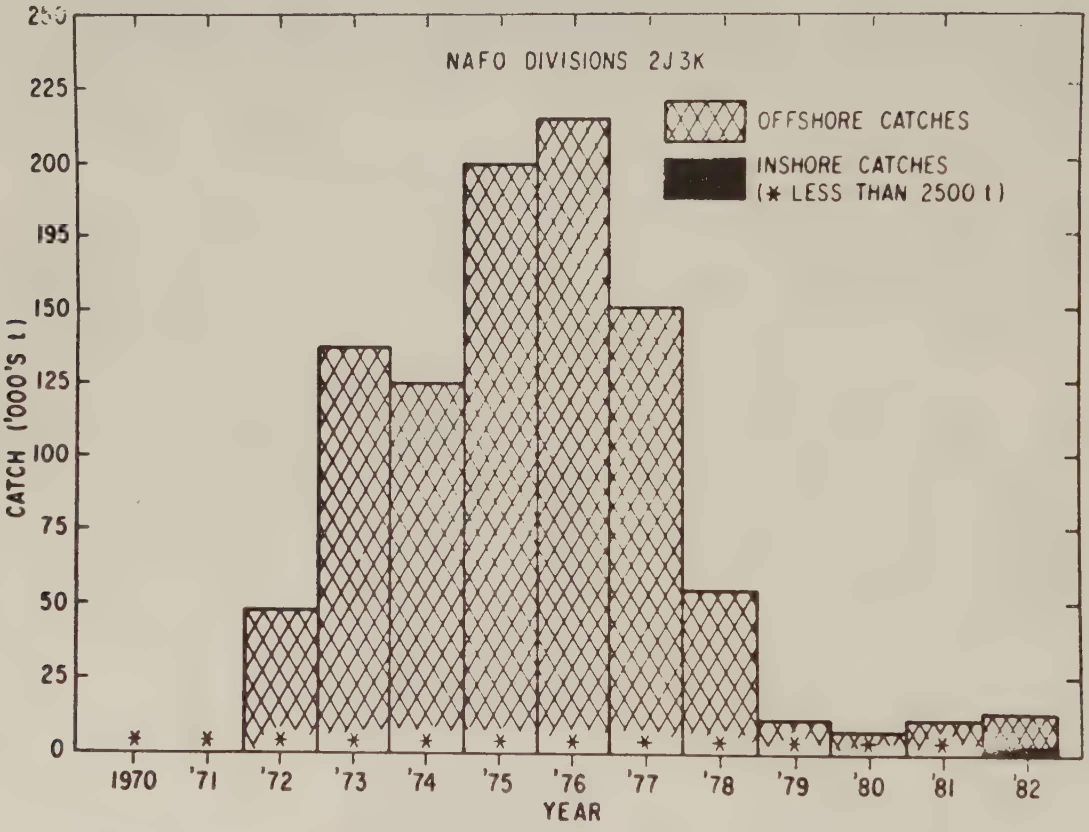


Fig. 4. Nominal catches of capelin in NAFO Div. 2J3K, 1970-1982. 1982 catch data are preliminary.

The management of capelin came under the jurisdiction of ICNAF, and later NAFO, until Canada extended its fisheries jurisdiction to 200 miles (January 1, 1977). At this time, the Div. 2J3K stock came solely under Canadian management because it occurred completely within Canadian jurisdiction although Canada has continued to request that biological advice be provided through NAFO. The Div. 3NO stock overlaps the Canadian zone and biological advice and management recommendations have continued under the auspices of NAFO. Biological advice for the Div. 3L stock continues to be provided through NAFO although all of the fishery occurs within the coastal zone. The biological advice provided for the management of capelin has, with few exceptions, been adopted by the fisheries managers in NAFO and in Canada and as a result, the biological advice and some of the rationale for that advice is provided below.

The biological advice, provided through ICNAF and later NAFO, was initially requested because of the increasing commercial offshore fishery during the early 1970's. The first advice concerning the total allowable catch (TAC) of capelin pertained to 1974 when it was recommended by the Standing Committee on Research and Scientists (STACRES) of ICNAF that the catch should not exceed 250,000 tons. The following year (1975) it was recommended that the total TAC could be increased to 500,000 tons and maintained for three years. Furthermore, it was noted that the fishery should be restricted to mature capelin approaching and during the spawning season and countries participating in the fishery should conduct surveys of both the adult and juvenile stock to monitor the effect of the fishery. Also in 1975, a crude estimate of relative stock sizes resulted in a recommendation that 300,000 tons could be allocated to the northern area (Div. 2J3K) and 200,000 tons to the southern area (Div. 3LNOPs). Further subdivision of the northern TAC was not practical at that time due to insufficient knowledge of stock separation. However, there was evidence to suggest that the fishery in Div. 3L was operating on several spawning components which spawn later inshore in Div. 3L, on the Southeast Shoal, and possibly in Div. 3Ps. It was recommended that only 10,000 tons be reserved for a TAC for Div. 3Ps, since this stock was believed to be small, but that this amount could be taken in Div. 3NO if not taken in Div. 3Ps. It was concluded that it would be desirable to concentrate the fishery as much as possible on the mature capelin in Div. 3NO to minimize potential adverse effects on capelin and other species. This would also reduce the possibility of overfishing any one of the spawning components present in Div. 3L earlier in the season and for the inshore spawning stock, it would minimize any adverse effect on the inshore migration and feeding success of the Div. 3L cod. The final subdivision of the 200,000 TAC in the southern stock was no more than 10,000 tons allocated to Div. 3Ps and no more than 50,000 tons allocated to Div. 3L with the remainder allocated to Div. 3NO. If these maxima were not achieved in Div. 3L and 3Ps, the uncaught amounts could be taken in Div. 3NO (Anon., 1975).

The biological advice remained essentially unchanged until 1979 when evidence of poor recruitment in the capelin population resulted in a recommendation of reductions in the TAC's. STACRES advised that the 1979 TAC in Div. 3LNO should be 16,000 tons and to protect the spawning stock in Div. 3N and during its migration through Div. 3O to Div 3N, there should be no commercial fishery for capelin in Div. 3NO. This meant that 16,000 tons could be taken only in Div. 3L. It was agreed by NAFO that there would be no offshore fishery for capelin in Div. 3L and Canada claimed only 10,000 tons to be taken inshore. Therefore, the quota for capelin in Div. 3L in 1979 was essentially 10,000 tons. In the northern stock, it was recommended that the 1979 TAC be reduced from 300,000 tons to 75,000 tons.

The recruitment prognosis remained poor in 1980 and the biological advice remained unchanged for the stocks in Div. 3LNO that is, a TAC of 16,000 tons with no fishing in Div. 3NO. In the north, the advice was to close the fishery or allow a small nominal TAC. It was noted that a small fishery of 10,000-15,000 tons in the north would allow scientists to better assess the status of the stock in 1980 and to quantify the advice for the next year. An experimental fishery with a TAC of 5,000 tons was conducted in the fall of 1980 to provide data for assessment purposes.

In 1981 there was some evidence of improvement in the southern area and based on the exploitation rate that had been recommended in 1980 and 1981, a TAC of 30,000 tons to be taken in Div. 3L was recommended while the Div. 3NO fishery should remain closed. In the northern area, there was conflicting evidence in the scientific data and as a result, the advice remained unchanged from the 1980 advice; that is, that the fishery remained closed or a small nominal fishery of 10,000-15,000 tons be allowed. An experimental fishery with a TAC of 10,000 tons operated in Div. 2J3K during the fall of 1981.

No scientific advice was requested for 1982 and the 1981 TAC's remained in effect for that year.

An assessment of the stocks conducted in mid 1982 (Anon., 1982) suggested that the stocks had improved dramatically, largely as a result of the strong 1979 year-class. The TAC recommended for the Div. 3L stock was 60,000 tons and for the Div. 2J3K stock, 50,000 tons. Although some improvement was detected in the Div. 3NO stock from surveys conducted in 1981, the abundance estimates were still much lower than historical estimates and it was recommended that this fishery remain closed in 1983.

In general terms, because of the uncertainties involved in the scientific data, the known poor recruitment to the capelin stocks during the late 1970's and early 1980's and the importance of capelin as a food for other marine species, a conservative exploitation rate of 10% has been recommended since 1979 for the Div. 3L stock. The TAC's recommended for the Div. 2J3K stock have been less than 10% of the projected biomass although no specific guideline (e.g. 10%) has been adopted.

POPULATION DYNAMICS AND FACTORS AFFECTING ABUNDANCE

There had been some studies on the biology of capelin (e.g. Templeman, 1948; Pitt, 1958b; Winters, 1966, 1970a, 1970b) but detailed information on population dynamics of capelin was not available during the early phases of the large offshore fishery. There have been three techniques used since the mid-1970's to assess the status of the capelin stocks in the Newfoundland area and describe the population patterns during the last decade; a surplus production model, acoustics methodology, and sequential capelin abundance models. The use of the three assessment methods has shown a trend over time. During the early phase of the fishery, acoustic estimates and the surplus production model were the only sources of information. Both types of estimates were recognized as being crude but they were used as indications of the magnitude of the capelin resource. The surplus production model was used only in the early years of capelin assessments whereas the acoustic method has been used since 1974. As the fishery continued through the 1970's, there were enough data accumulated to develop the sequential capelin abundance models. In the most recent years up to and including 1981, these models have been used as the most reliable indications of stock status and as a starting point for projections. Ironically, these models have depended on the fishery as a data source and the results from the models were largely responsible for the advice to reduce the total allowable catch.

The surplus production model was first developed in 1973 (Campbell and Winters, 1973) and expanded in 1975 (Winters, 1975; later revised by Winters and Carscadden, 1978). Although it is extremely crude, the model was used to provide biological advice and was intended to provide a first estimate of potential long-term annual yield of capelin. It was recognized that many species of marine fish, mammals and seabirds feed extensively on capelin and that the stocks of many of these predators had declined during the 1950's and 1960's. Therefore, it was assumed that there would be capelin available to a commercial fishery in the 1970's that previously would have been necessary to sustain the predator stocks. Cod, whales, and seals were chosen for this analysis because there were estimates of their abundance and of capelin consumption (albeit crude in some cases) by these animals. This model has recently been criticized (Beddington et al., 1981) as a management tool because it is over-simplified. Although this criticism is probably valid, it should be noted that the developers of the model stressed that the estimate of surplus production be interpreted only as indicative of the order of magnitude of potential capelin yield under the assumptions used in the model, most of which could not be tested. Furthermore, the TAC that was eventually put in force was 500,000 tons, twice the level proposed by the authors based on the estimates from the surplus production model.

Acoustic estimates, using echo integration, have been produced primarily by Soviet (Serebrov et al., 1975; Bakanev et al., 1976; Seliverstov and Kovalev, 1976; Kovalev et al., 1977; Klochkov et al., 1977; Bakanev and Seliverstov, 1978; Klochkov and Seliverstov, 1978; Ermolchev et al., 1979; Seliverstov and Serebrov, 1979; Ermolchev et al., 1980; Bakanev 1980, 1981; Bakanev and Ermolchev, 1982) and Canadian (Miller et al., 1978; Miller and Carscadden, 1979a; Carscadden and Miller, 1980; Miller and Carscadden, 1980, 1981; Miller et al., 1982) scientists although one early estimate (Dragesund and Monstad, 1973) was produced from an exploratory survey by the Norwegians. The Soviets have the longest time-series of acoustic estimates of capelin, beginning in 1974 in the northern area (Div. 2J3K) and 1975 in the southern area (Div. 3LNO). The Canadian estimates are more recent with the first estimate in the northern area coming from a 1977 survey and in the southern area from a 1979 survey. In most recent years, except for 1982, the acoustic estimates are used not as absolute estimates but as trend indicators. The decision to use the Canadian acoustic estimates as relative indicators of stock status arose for three reasons. First, there were relatively few measurements of target strength available for capelin; the target strength values are critical for biomass estimation and errors in target strength produce proportional errors in the final biomass estimate. There was no information available on swimming angle of capelin in the field and it is known that target strength can change radically with swimming angle of the fish (Nakken and Olsen, 1977). Second, the personnel collecting the acoustics data and estimating biomass from these data were, at first, relatively inexperienced in this field. As a result there was a period of learning associated with the acoustics methodology which ran parallel to the accumulation of basic biological data to be used in the development of acoustic techniques (e.g. survey design) specifically for capelin. Third, there was a reluctance on the part of other scientists to accept estimates derived from acoustics, a relatively new technology to most, as valid indications of stock status. Although the problems associated with target strength and swimming angle have not been fully resolved, considerable experience has been gained by the Canadian investigators and at the same time other scientists have become more familiar with the advantages and disadvantages of acoustic techniques. In 1982, acoustic estimates were used as absolute estimates (still recognizing the potentially large sources of error associated with target strength) and as a basis for projections (Anon., 1982).

The sequential capelin abundance models (Carscadden et al., 1978; Carscadden and Miller, 1979; Miller and Carscadden, 1979b; Carscadden and Miller, 1980; 1981; Carscadden et al., 1981) which have provided a historical perspective of the dynamics of capelin in the Newfoundland area were developed because the high natural mortality of capelin prevented the use of standard sequential population analysis such as virtual population analysis (Gulland, 1965) or cohort analysis (Pope, 1972). The sequential capelin abundance models (SCAM) are similar to VPA and cohort analysis both in their design and mechanisms. They attempt to calculate for any year-class its age-specific size and fishing mortality rate based on such input parameters as catch-at-age and natural mortality rate. Like cohort analysis, some method of estimating fishing mortality in the most recent years is necessary and in all cases to date, commercial catch rates have been used to calibrate the models and so provide an estimate of terminal fishing mortality. The models differ from cohort and VPA in that some temporal partitioning occurs and the different mortality rates (i.e. high spawning mortality rate at the time of the year and natural mortality rate at other times) are applied to the population estimates at the appropriate time of the year within the model. Since recruitment to the mature portion of the population is essentially equivalent to maturation rate and the fishery operates primarily on mature fish it was necessary to incorporate annual age-specific maturation rates into the models as well. The sensitivity of the models is presently being quantified, however, it is known that they are sensitive to some of the input parameters, e.g. proportions mature-at-age and undoubtedly, like cohort analysis, they are less reliable in most recent years. However, for this discussion, it is assumed that they provide a reasonably accurate representation of capelin population dynamics over the last decade.

The sequential capelin abundance models have been useful for two stocks - Div. 2J3K (SCAM 2J3K) and Div. 3L (SCAM 3L) for 1972-1980. The results of SCAM 2J3K (Carscadden and Miller, 1981) are shown in Table 1 and Fig. 5. The results of this model were not accepted by assessment scientists (Anon., 1982) for biomass estimates in 1981 because the fishing mortality rates estimated in the most recent years were very low (F = 0.01). Instead acoustic estimates for 1981 were used (Table 1, Fig. 5) and therefore, some caution should be exercised in comparing the 1981 estimates with estimates from previous years because of the different methods of assessment. The results of the model indicate that total biomass (Jan. 1) varied between 870,000 tons and 3,697,000 tons between 1972 and 1980 with the biomass peaking in 1975 and 1976. During the same time period, the total biomass at the approximate start of fishing (Sept. 1) varied between 428,000 tons in 1980 and 4,025,000 tons in 1975. For this stock, exploitable capelin biomass on Sept. 1 was calculated by multiplying estimated population numbers-at-age by a calculated partial recruitment factor for each age. This partial recruitment factor was estimated by expressing fishing mortality rate at age each year as a proportion of the highest fishing mortality rate in that year (Carscadden and Miller, 1981). No estimate of exploitable biomass was available for 1981, but between the years 1972 and 1980, the peak biomasses occurred in 1975 and 1976 and declined after that. The results from the acoustic survey suggest that the total biomass (Sept. 1) in 1981 increased by a factor of approximately 4 times from the low abundance in 1978 and 1979. The large biomasses in the mid 1970's were the result of the strong 1973 year-class. The next strongest year-class was the 1969 year-class which resulted in biomasses at intermediate levels in the early 1970's. The 1974-1978 year-classes were very small and the biomass declined during the late 1970's.

Table 1: Numbers of fish (billions) and biomass at 1 Jan. and 1 Sept., 1972-80 from SCAM 2J3K (Carscadden and Miller, 1981) and acoustic survey (Miller *et al*., 1982) autumn 1981.

Age/Year	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
TOTAL POPULATION AT START OF YEAR										
2	52.2	53.0	42.1	224.4	22.2	7.7	6.4	18.0	62.5	
3	60.5	38.4	38.0	30.2	161.0	15.7	5.6	4.5	13.0	
4	24.5	37.6	24.5	21.8	16.3	81.8	8.7	3.1	2.9	
5	2.4	7.8	15.2	10.3	4.5	3.6	26.9	2.8	.5	
6	.4	.5	1.6	3.8	1.4	.5	1.0	5.2	.5	
Biomass (tons)	1,987,000	2,220,000	2,274,000	3,697,000	3,642,000	2,435,000	1,238,000	501,000	870,000	
TOTAL POPULATION (1 Sept.)										
2	42.7	43.4	34.4	183.7	18.2	6.3	5.3	14.7	51.2	71.0
3	42.9	28.6	26.7	20.6	98.1	11.2	4.3	3.3	9.2	10.0
4	9.1	19.0	12.3	5.8	4.6	33.1	3.7	.6	1.1	2.0
5	.6	2.1	4.9	1.7	.6	1.5	6.3	.5	.1	1.0
6	.1	.1	.4	.3	.1	.2	.1	.5	.1	1.0
Total biomass (tons)	1,987,000	2,251,000	1,848,000	4,025,000	2,843,000	1,474,000	434,000	428,000	1,177,000	1,794,000
Exploit. biomass (tons)	485,000	1,048,000	984,000	1,516,000	1,613,000	644,000	245,000	334,000	169,000	

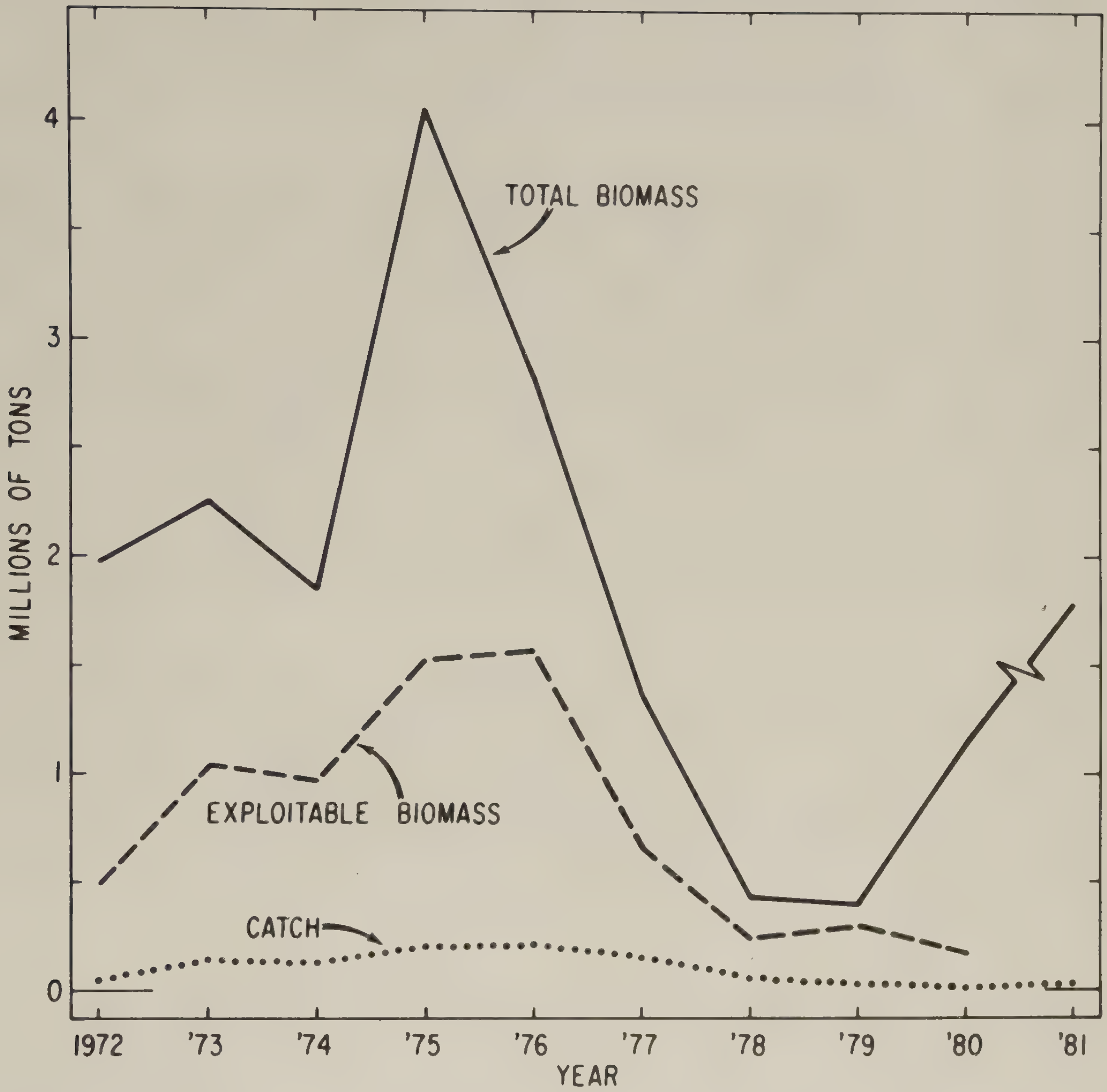


Fig. 5. Estimates of total biomass (1 Jan.) and exploitable biomass (1 Sept.), 1972-80 from SCAM 2J3K acoustic estimate (fall 1981) and catch for Div. 2J3K capelin stock.

The 1979 year-class appears stronger than the 1974-1978 year-classes; this year-class has appeared in abundance as immature fish during research vessel surveys. Although the 1982 data have not been analyzed completely, observations from our surveys, from other scientists and from fishermen around the Island indicate that the spawning biomass of capelin significantly increased in 1982 and this was due largely to the 1979 year-class. An examination of the catches (Fig. 5) over the 1972-1981 period suggests that catches were very low in relation to the biomass available.

The results of the analysis using SCAM 3L are given in Table 2 and Fig. 6. It should be emphasized that these estimates are considered less reliable than the results for the Div. 2J3K stock using SCAM 2J3K. Estimates from the Div. 3L model could be calculated only up to 1977 because of a lack of reliable independent estimates of abundance in most recent years. Estimates of abundance for 1978-1981 are based on predicted values of year-class strength at age 3 derived from a relationship between year-class strengths in the Div. 2J3K and Div. 3L stocks (Carscadden and Miller, 1979; Carscadden et al., 1981) which suggests that parallelism in year-class strength of capelin occurs in all areas of the northwest Atlantic. Estimates of abundance for 1981 acoustic surveys (Miller et al., 1982) suggested a total biomass of 1,764,000 tons (ages 1-6) and 1,103,000 tons of age 3 fish and older in Div. 3L, or approximately 3.5 times the projected estimate from Carscadden et al., 1981). The results of a Soviet acoustic survey (Bakanev and Ermolchev, 1982) estimated approximately 421,000 tons of immature capelin in Div. 3L and northern Div. 3N. Unfortunately this estimate is not strictly comparable to the Canadian estimate because very few older mature capelin were observed. The Canadian survey was conducted closer to the coast and undoubtedly detected significant numbers of age 3 fish and older (compare the estimated numbers of 1973 year-class in the two surveys) that were migrating inshore to spawn.

The capelin stock in Div. 3L was highest in abundance in the mid 1970's and intermediate in abundance in the early 1970's, largely due to the strongest year-classes, the 1973 and 1969 year-classes. According to the estimates of biomass for the late 1970's shown in Table 2 (assuming the parallelism of year-class strengths), the biomass dropped during this period. Although the acoustic estimates from the late 1970's were never used as absolute for assessment purposes, the trends were taken as indicative of stock status and support the results of SCAM 3L. The 1979 year-class was also relatively strong in this area resulting in a higher spawning biomass in 1982. As in the Div. 2J3K stock, the catches in Div. 3L have been relatively low in relation to the estimates of capelin biomass for this stock.

Thus, for both the northern (Div. 2J3K) and southern (Div. 3LNO) areas, the large commercial capelin fishery that operated during the 1970's grew very rapidly, peaked in the mid 1970's and declined rapidly in the late 1970's; this fishery pattern coincided with the pattern of capelin biomass. The catch levels declined as the population biomass declined because of poor year-classes between 1974 and 1978. The fact that the peak catches of the fishery occurred during the years in which small year-classes were produced tends to implicate the fishery in the decline. In fact, the fishery has been cited as a probable contributing factor only in the decline of the Div. 3NO stock (Anon., 1979). The analyses that have been conducted to date for the Div. 3L and Div. 2J3K stocks suggested the catch was not large in relation to the biomass available and therefore, was unlikely to have had deleterious effects on the capelin stocks. Furthermore, the 1979 year-class, which appears to be large, resulted from the spawning in a year in which both the capelin biomass and the fishery were small.

Although the factors affecting the variation in year-class strength of capelin are not fully understood, there is evidence available to suggest that environmental factors operating on the early stages of the life history are affecting survival and therefore recruitment. Frank and Leggett (1981a, b; 1982a, b) have been studying factors affecting capelin egg and larval mortality on a capelin spawning beach in Newfoundland since 1978. The time between egg deposition on the beach and hatching in the gravel was influenced by average incubation temperature; this incubation temperature varied between years and between cohorts in a single year and between low, mid, and high tide locations on the beach. Water temperature, maximum and minimum air temperatures and hours of sunlight all determined the average incubation temperatures. The interacting effects of egg density, water temperatures, maximum and minimum air temperature, hours of sunlight, rainfall and tidal amplitude explained over 70% of the temporal and spatial variance in

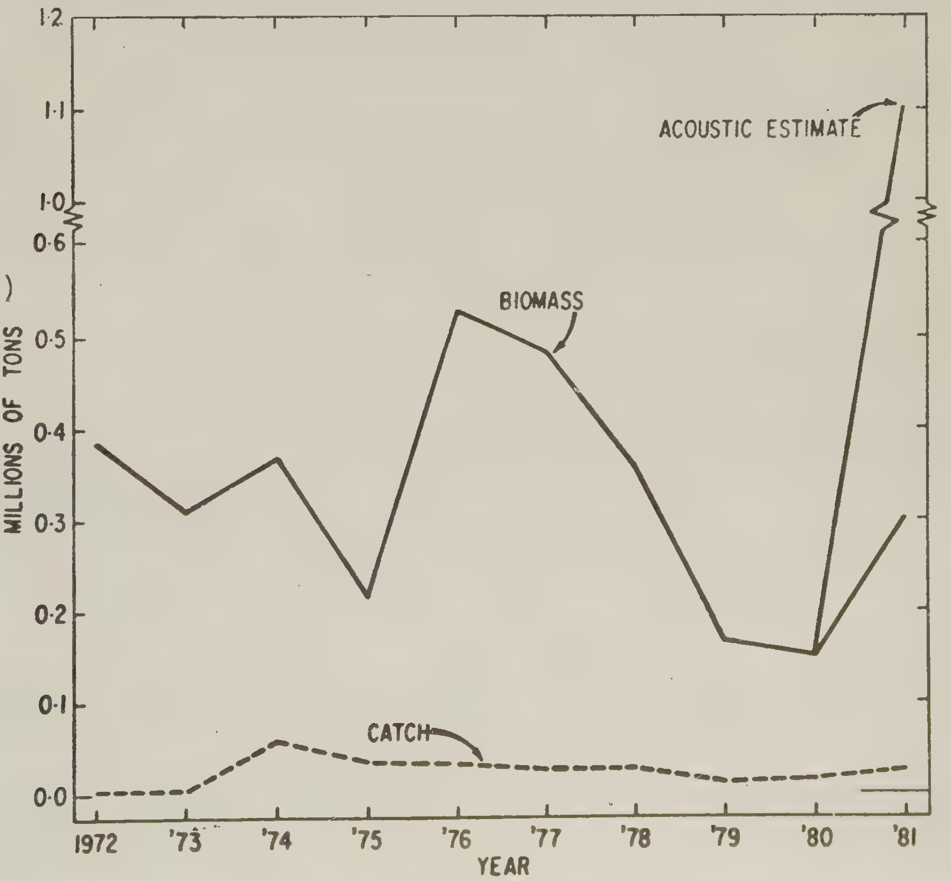
Table 2. Numbers of fish (billions) and biomass at 1 Jan. and 1 Sept., 1972-81 from SCAM 3L (Carscadden *et al.*, 1981) and from acoustic surveys, June 1981 (Miller *et al.*, 1982; Bakanev and Ermolchev, 1982; Anon., 1982) for capelin *in* Div. 3L.

Age/Year	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
TOTAL POPULATION AT START OF YEAR (SCAM 3L)										
3	12.7	9.0	8.2	5.1	24.5	9.9	5.1	5.0	6.0	9.9
4	3.9	6.1	4.7	3.0	1.8	13.1	5.3	2.4	2.4	2.8
5	.3	.8	3.0	.5	.3	.4	4.7	1.1	.5	.5
Biomass (tons)	386,000	311,000	368,000	216,000	529,000	483,000	358,000	167,000	150,000	302,000

TOTAL POPULATION (ACOUSTIC), June 1981

Age	CANADIAN	USSR
1	43.0	42.9
2	33.0	42.1
3	45.0	3.1
4	10.0	.3
5	3.0	.2
6	1.0	-
Total biomass (tons)	1,764,000	421,000
3+ biomass (tons	1,103,000	

Fig. 6. Estimates of total biomass (1 Jan.) 1972-81 from SCAM 3L acoustic estimate (June 1981) and catch for Div. 3L capelin stock.



egg mortality. The climatic and hydrographic variables that influence egg mortality vary only slightly over most of the major spawning sites in eastern Newfoundland and southern Labrador areas and the authors suggest that synchronous changes in these variables may contribute to the annual fluctuations in capelin year-class strength (Frank and Leggett, 1981b).

Capelin eggs hatch in the gravel and the larvae remain there until washed into the near-shore environment by wave action (Frank and Leggett, 1981a). Larval growth during the residence in the gravel was regulated by the interacting effects of water temperature and hours of sunlight. The swimming performance of the larvae on their release into the water was directly related to their condition which in turn was negatively related to the length of time spent in the beach gravel and to the temperature conditions during that time (Frank and Leggett, 1982a).

The emergence of larval capelin from beach gravel was correlated with onshore wind-induced wave action (Frank and Leggett, 1981a). There was a positive correlation between density of larvae in the beach gravel and the length of time separating the occurrence of onshore winds. The onshore winds that were instrumental in releasing the larvae from the gravel also induced rapid water mass exchange in the inshore waters and as a result, cold, high-saline, predator-laden waters which were present during periods of offshore winds were replaced with warmer, less-saline waters, which contained more potential prey (Frank and Leggett, 1982b). Thus, the net effects of the onshore winds were to facilitate the release of larvae from the gravel and their entry into the nearshore waters; to induce water mass changes in the nearshore waters such that the resulting waters were warmer and less-saline; to cause a 3-20 fold reduction in the potential predator complex; to increase the potential food resource for larval capelin by 2 to 3 times. Furthermore, Frank and Leggett (1982b) reported that the release of large numbers of capelin coupled with the reduction of predators during onshore winds resulted in predator satiation. As a result, the capelin larvae initiate their drift in an environment that is predictable with respect to wind conditions and consistent over the species range in Newfoundland (Frank and Leggett, 1982b). However, the timing and the frequency of these onshore winds is unpredictable and of low frequency since the summer winds in Newfoundland are generally offshore (Frank and Leggett, 1982b).

Data available for two years, 1978 and 1979 (Frank and Leggett, 1981a) indicate that egg densities in the gravel were similar. However, the frequency of onshore winds during the hatching period was 50% greater and larval densities in the nearhsore environment were 60% greater in 1979. This increase in larval density also agreed with the observation that the proportion of larvae exiting the beach in good physical condition in 1979 was higher than 1978. These findings are interesting when compared to the estimates of biomass of adult capelin (Fig. 5 and 6) for 1978 and 1979 and year-class strengths resulting from these spawnings. Adult biomass in both 1978 and 1979 was low but there was an increase in released larvae in good physical condition in 1979, because of a greater frequency of onshore winds, and the 1979 year-class is apparently larger than the 1978 year-class. The spawning biomass of capelin in 1982 was much improved, largely because of the contribution of the 1979 year-class.

Once released from the beach gravel into the pelagic environment, the larval capelin are transported quickly from the immediate beach area and into the onshore waters (W.C. Leggett, pers. comm.). During the next few months, they are restricted to surface waters (Jacquaz et al., 1977; Fortier and Leggett, 1983) where growth and survival are probably influenced by prevailing hydrographic conditions. We have assumed that hydrographic conditions during this larval phase in the surface layers influence recruitment and have recently begun investigating the relationship between recruitment and two hydrographic variables, temperature and salinity. Preliminary results from these investigations are reported here. The temperature data are from Station 27 (47°32'50"N. 52°35'10"W), located off St. John's, Newfoundland and estimates of year-class strength of capelin as two-year-olds from northern (Div. 2J3K) stock (Table 1) were used as estimates of recruitment. Although the temperature data are not from exactly the same area, the Labrador current is the dominant hydrographic feature in the Div. 2J3K area and the Station 27 area; hence, the temperatures at Station 27 should reflect temperature trends in the northern area. Temperatures used were the sums of the monthly means for July-December from surface to a depth of 20 m (S. Akenhead, pers. comm.). The abundance of the 1969 year-class as two-year-olds was estimated from the abundance of three-year-olds using the same assumptions as in the model. The recruitment data were transformed to natural logarithms because Hennemuth et al. (1980) reported that recruitment in most of the fish stocks they investigated exhibited a lognormal pattern. There was a significant relationship (Fig. 7) between recruitment (R) and water temperature (TEMPSUM) ($\ell nR = 11.74 + 0.27$ TEMPSUM, $r = 0.71$). Although the time series is relatively short, the relationship was tested using detrended data (Box and Jenkins, 1976). The data were detrended by taking differences:

$$\ell nR_0 = nR_t - nR_{t-1}$$

$$\mathrm{TEMPSUM}_0 = \mathrm{TEMPSUM}_t - \mathrm{TEMPSUM}_{t-1}$$

where R_t is recruitment in year t and T_t is temperature summed in year t. The relationship was still positive ($\ell nR_0 = -0.03 + 0.21\ \mathrm{TEMPSUM}_0$, $r = 0.66$) but was not quite significant at the 5% level (Fig. 7).

The association between surface salinity and recruitment was also tested using salinity values from Station 27 over the same time period. There was no significant relationship between salinity and recruitment.

It is possible that predation has some influence on year-class variation in capelin and Dawe et al. (1981) investigated the effect of inshore predation by squid (*Illex illecebrosus*) on the abundance of capelin using correlation analysis. Squid are summer migrants into the Newfoundland area. Their populations fluctuate widely from year-to-year and while in the inshore area, they feed heavily and grow rapidly. In the analysis, the authors found a negative correlation between the abundance of squid and year-class strength (ages 0+1) of Div. 2J3K capelin. However, they noted that there was a number of problems with their analysis, usually related to the unavailability of proper data to evaluate their hypothesis. For instance, there are no quantitative studies on squid feeding and although squid appear to have the potential to have a significant impact on prey species, the biomass of the prey species cannot be calculated because it is not known if squid prey on larvae, 0-group, 1-group or older fish. The authors were forced to use estimates of capelin year-class size at ages 2,3, or 4 as indicators of abundance of age groups 0 and 1 since neither estimates of abundance of the younger age groups nor estimates of natural mortality were available. The analysis may have been confounded by temporal trends since the time series for capelin was only 8 years. In this respect it is interesting to note that in 1979, squid abundance was very high (Dawe et al., 1981) while the 1979 year-class of capelin appears to be good. Thus, this correlation may disappear with the addition of the 1979 point. Furthermore, recent squid feeding data suggests that capelin are not important components of the diet of squid during the inshore phase of the life cycles of both species (E.G. Dawe, pers. comm.).

AFFECTS OF CAPELIN FLUCTUATIONS ON COMPETITOR AND PREDATOR STOCKS

Although the trends in abundance of capelin during the last decade are known, there is very little information on the effects of the fluctuations on possible competitor and replacement species. In the southern part of the capelin range, the only resident species that might be considered to occupy a similar niche is sand lance (*Ammodytes dubius*) while in the north this position would be taken by arctic cod (*Boreogadus saida*). While there are no detailed quantitative data available for these species, it appears that the populations of sand lance (G.H. Winters, pers. comm.) and arctic cod (H. Lear, pers. comm.) did increase during the late 1970's when capelin abundance had declined. It is interesting to note that the increase in arctic cod, whose normal distribution is much further north than that of capelin, and the decrease in capelin abundance occurred during a time when colder water temperatures predominated (Fig. 7).

Vesin et al. (1981) noted that the abundance of squid (*Illex illecebrosus*) was high when capelin abundance was low and they estimated that with the decline of capelin in the Newfoundland area in the late 1970's, substantial quantities of zooplankton would be released to other predators. This led them to speculate that this release of zooplankton may be important in regulating changes in year-class of other species, notably arctic cod and squid. Except for the estimates of surplus zooplankton, no quantitative analyses were presented to support the hypothesis.

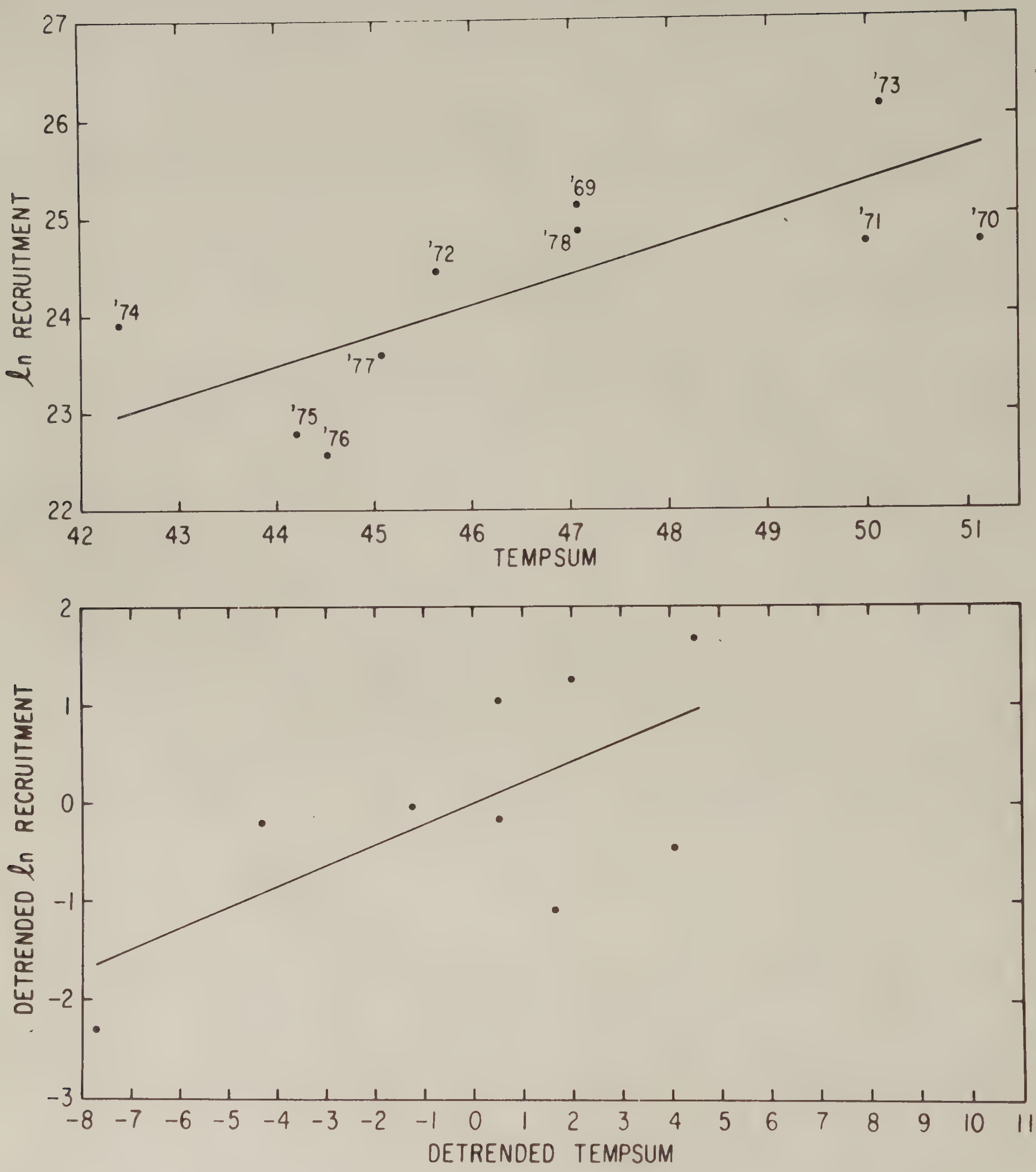


Fig. 7. Relationship between recruitment and water temperature.
Top: ℓn recruitment vs. TEMPSUM
Bottom: detrended ℓn recruitment vs. detrended TEMPSUM
(see text for details)

A great deal of concern has been expressed about the effects of fluctuations in capelin abundance on predator stocks and this has prompted scientific studies using existing data on two of these relationships - capelin and cod (*Gadus morhua*), and capelin and salmon (*Salmo salar*). The effects of fluctuations of capelin biomass on cod growth and on the inshore cod fishery were investigated by Akenhead et al. (1982). There was no statistically significant effect of capelin biomass on cod growth detected. However, after making corrections for the biomass of cod, the authors did detect significant relationships between cod trap catches versus capelin biomass as well as between total inshore gear catches versus capelin biomass and water temperature. However, there were a number of uncertainties in the data and the authors suggested that the statistically significant relationships not be accepted as unequivocal proof that such relationships do exist in nature but that they be used to determine the direction of future research.

Recently, the failure of the 1977 smolt-class of salmon prompted Carter (1979, 1980) to state that the decline of capelin due to overfishing caused the failure of this smolt-class. It appeared that an unusually high mortality of this smolt-class had occurred during its first winter at sea (Reddin and Carscadden, 1981). There were virtually no feeding data available to indicate whether capelin were important in the diet of salmon during their first sea-winter but the size of young capelin in relation to smolts suggested that they would be suitable prey. Assuming that capelin were eaten by salmon, Reddin and Carscadden (1981) showed, using correlation analyses, that in some cases there were statistically significant relationships between salmon catches and abundance of young capelin. However, the authors noted that these relationships were significant only because of the 1977 smolt-class. Indeed, when the analyses were repeated (Carscadden and Reddin, 1982) using data updated by one year, none of the relationships was statistically significant.

The analyses of the cod-capelin and salmon-capelin relationships failed to produce unequivocal proof of the dependence of the predator on capelin. In both analyses, the data available were not collected to test the postulated relationships, thereby making the results suspect, or in some instances, the proper data were not available. For instance, cod trap catches were assumed to be an indicator of inshore cod abundance which further assumes that fishing effort has not changed over the time period in question. A better indicator would have been catch per effort to account for annual changes in effort unfortunately effort data were not available. In both studies, it was assumed that the predators were dependent on capelin and a change in the abundance of capelin would result in the dynamics of the predator. However, the diet of both cod (Akenhead et al., 1982) and adult salmon (Reddin and Carscadden, 1982) is spatially and temporally variable and in the absence of capelin, both species would feed on other prey if available. In this case, an absence of capelin probably would not result in starvation of the predator nor an immediate drop in abundance. Instead, a reliance on other prey or less prey might result in slower growth and/or reduced fecundity, if in fact there was a detrimental effect at all. Such effects would be subtle and long-term making them difficult to detect.

ACKNOWLEDGEMENTS

D.S. Miller has contributed significantly in the development of and computer programming for the acoustic techniques and sequential capelin assessment models. G.H. Winters has provided valuable advice and helped in the development of the sequential capelin abundance models. Scott Akenhead provided the monthly Station 27 data, 0-20 m. None of the information presented here would have been possible without the capable assistance of a number of technicians in the Pelagic Section, Fisheries Research Branch, St. John's.

REFERENCES

Akenhead, S.A., J.E. Carscadden, H. Lear, G.R. Lilly and R. Wells. 1982. Cod-capelin interactions off northeast Newfoundland and Labrador. p. 141-148. *In* Multispecies approaches to fisheries management advice. (M.C. Mercer, ed.). Can.Spec.Publ.Fish.Aquat.Sci. 59:169 p.

Anon. 1975. Int.Comm.Northwest Atl.Fish.Redbook. STACRES Spec.Meet. Jan. 1975.

___________. 1979. Int.Comm.Northwest Atl.Fish.Redbook. STACRES Spec.Meet. Feb. 1979.

___________. 1982. Rep.of Scientific Council. NAFO SCS Doc. 82/18, Ser.No. N577, 77 p.

Bailey, R.J.F., K.W.Able and W.C. Leggett. 1974. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St. Lawrence estuary and western Gulf of St. Lawrence. J.Fish.Res.Board Can. 34:2030-2040.

Bakanev, V.S. 1980. Results of USSR investigations on capelin in Divisions 2J and 3K, Autumn 1979. NAFO SCS Doc. 80/43. Ser.No. NO75. 6 p.

___________. 1981. Results of Soviet investigations on capelin in Northwest Atlantic in 1980. NAFO SCR Doc. 81/II/10. Ser.No. N274, 10 p.

Bakanev, V.S. and V.A. Ermolchev. 1982. Hydroacoustic assessment of capelin abundance in NAFO Divisions 3LNO in May-June 1981. NAFO SCR Doc. 82/61, Ser.No. N554, 10 p.

Bakanev, V.S. and S.A. Seliverstov. 1978. Capelin investigations in the waters off southern Labrador (Division 2J) and on the north Newfoundland Bank (Division 3K) in the autumn of 1977. ICNAF Res.Doc. 78/30, Ser.No. 5191, 11 p.

Bakanev, V.S., S.A. Seliverstov and L.I. Serebrov. 1976. Preliminary instrument estimate of abundance and biomass of capelin off south Labrador and the north Newfoundland Bank (Divisions 2J and 3K). ICNAF Res.Doc. 76/VI/54, Ser.No. 3840, 16 p.

Barnes, M. 1974. Preface to Final Report of 1973 Newfoundland Inshore Capelin Development Program by Andrew Duthie, Industrial Development Branch, Newfoundland Region, St. John's Newfoundland.

Beddington, J., D. Botkin and S.A. Levin, 1981. Mathematical models and resource management. p. 1-5. *In* Renewable Resource Management, Proceedings of a Workshop on Control Theory Applied to Renewable Resource Management and Ecology. Lecture Notes in Biomathematics No. 40, Springer-Verlag. N.Y.

Box, G.E.P. and G.M. Jenkins. 1976. Time series analysis, forecasting and control. Holden-Day, Toronto.

Campbell, J.S. and G.H. Winters. 1973. Some biological characteristics of capelin, *Mallotus villosus*, in the Newfoundland area. ICNAF Res.Doc. 73/90, Ser. No. 3048, 8p.

Carscadden, J.E. and D.S. Miller. 1979. Biological aspects of capelin and a sequential capelin abundance model for the Division 3LNO stock. ICNAF Res.Doc. 79/II/33, Ser.No. 5359, 20 p.

___________. 1980. Analytical and acoustic assessments of the capelin stock in Subarea 2 and Div. 3K, 1979. NAFO SCR Doc. 80/13, Ser.No. NO45, 19 p.

___________. 1981. Analytical assessment of the capelin stock in Subarea 2 + Div. 3K using SCAM. NAFO SCR Doc. 81/4, Ser. No. N268, 8 p.

Carscadden, J.E., D.S. Miller, and G.H. Winters. 1978. Biological aspects of the Div. 3NO capelin stock in 1977 and a capelin sequential abundance model. ICNAF Res.Doc. 78/VI/52, Ser.No. 5217. 20 p.

Carscadden, J.E. and R.K. Misra. 1980. Multivariate analysis of meristic characters of capelin (*Mallotus villosus*) in the northwest Atlantic. Can.J.Fish.Aquat.Sci. 37:725-729.

Carscadden, J.E. and D.G. Reddin. 1982. Salmon-capelin interactions: here today, gone tomorrow. CAFSAC Res.Doc. 82/23. 10 p.

Carscadden, J.E., G.H. Winters and D.S. Miller. 1981. Assessment of the Division 3L capelin stock NAFO SCR Soc. 81/VI/25, Ser.No. N304, 14 p.

Carter, W.M. 1979. Where have all the salmon gone? Int.Atl.Salmon Found.Newsletter 9(4).

__________. 1980. Capelin and Atlantic Salmon. Int.Atl.Salmon Found. Newsletter 10(1).

Dawe, E.G., G.R. Lilley and J.A. Moores. 1981. An examination of the influence of squid (Illex illecrbrosus) on recruitment in several finfish stocks off eastern Newfoundland and Labrador. NAFO SCR Soc. 81/VI/25, Ser.No. N304, 14 p.

Dragesund, O. and T. Monstad. 1973. Observations on capelin (Mallotus villosus) in Newfoundland waters. ICNAF Res.Doc. 73/33. Ser.No. 2967, 14 p.

Ermolchev, V.A., S.M. Kovalev and A.S. Seliverstov. 1979. Methods and results of echometric surveys on the assessment of the Grand Newfoundland Bank capelin abundance in spring-summer 1979. ICNAF Res.Doc. 79/31, Ser. No. 5357, 11 p.

Ermolchev, V.A. S.M. Kovalev, V.S. Mamylov and A.S. Seliverstov. 1980. Assessment of capelin stocks in Divisions 3LNO in May-June 1979. ICNAF Res.Doc. 80/42, Ser.No. N074, 9 p.

Fortier, L. and W.C. Leggett. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. In review Can.J.Fish.Aquat.Sci.

Frank, K.T. and W.C. Leggett. 1981a. Wind regulation of emergence times and early larval survival in capelin (Mallotus villosus). Can.J.Fish.Aquat.Sci. 38:215-223.

__________. 1981b. Prediction of egg development and mortality rates in capelin (Mallotus villosus) from meteorological, hydrographic, and biological factors. Can.J.Fish.Aquat.Sic. 38:1327-1338.

__________. 1982a. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (Mallotus villosus) and its application to the match/mismatch hypothesis. Can.J.Fish.Aquat.Sci. 39:691-699.

__________. 1982b. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (Mallotus villosus). Can.J.Fish.Aquat.Sci. 39:991-1003.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. Cons.Perm.int.Explor.Mer, 1965. CM, Doc. No. 3.

Jacquaz, B., K.W. Able and W.C. Leggett. 1977. Seasonal distribution, abundance, and growth of larval capelin (Mallotus villosus) in the St. Lawrence estuary and northwestern Gulf of St. Lawrence. J.Fish.Res.Board Can. 34: 2015-2029.

Jangaard, P.M. 1974. The Capelin (Mallotus villosus) biology, distribution, exploitation, utilization and composition. Bull.Fish.Res.Board Can. 186:70 p.

Klochkov, D.N., and A.S. Seliverstov. 1978. Assessment of abundance and biomass of the spawning stock of capelin in ICNAF Division 3N in summer of 1977. ICNAF Res.Doc. 78/29, Ser. No. 5190, 6 p.

Klochkov, D.N., A.S. Seliverstov and L.I. Serebrov. 1977. Estimate of capelin stocks in the south Labrador and northern Newfoundland Bank areas in the autumn of 1976 (Divisions 2J and 3K). ICNAF Res.Doc. 77/33, Ser.No. 5058, 11 p.

Kovalev, S.M., A.S. Seliverstov and M.L. Zaferman. 1977. Size of a spawning capelin stock on the Grand Newfoundland Bank (Div. 3N) in 1976 (South-Western Stock). ICNAF Res.Doc. 77/32, Ser.No. 5057, 8 p.

Lear, W.H. 1969. The biology and fishery of the Greenland halibut (Reinhardtius hippoglossoides) in the Newfoundland area. M.Sc. Thesis, Memorial University of Newfoundland, 1969.

__________. 1972. Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. Int.Comm.Northwest Atl.Fish.Res.Bull. No. 9:27-29.

Lewis, H.F. 1937. Notes on the birds of the Labrador peninsula in 1934 and 1935. Can.Field Natur. 51(7):99-105.

Lien, J. 1980. Whale entrapment in inshore fishing gear in Newfoundland. Final Report to Fisheries and Oceans, Canada.

Lilly, G.R. 1981. Influence of the Labrador Current on predation by cod on capelin and sand lance off eastern Newfoundland. Northwest Atl.Fish.NAFO Sci.Coun. Studies 3:77-82.

Lilly, G.R., R. Wells and J. Carscadden. 1981. Estimates of the possible consumption of capelin by the cod stocks in Divisions 2J + 3KL and 3NO. NAFO SCR Doc. 81/8. Ser.No. N272, 9 p.

Miller, D.S. and J. Carscadden. 1979a. An acoustic estimate of capelin biomass in ICNAF Divisions 2J and 3K. October 1978. ICNAF Res.Doc. 79/34, Ser. No. 5360, 8 p.

__________. 1979b. Biological characteristics and biomass estimates of capelin in ICNAF Divs. 2J + 3K using a sequential capelin abundance model. ICNAF Res.Doc. 79/32, Ser.No. 5358, 15 p.

__________. 1980. An acoustic survey of capelin (Mallotus villosus) in Divisions 3LNO, 1979. NAFO SCR Doc. 80/4, Ser.No. NO46, 8 p.

__________1981. Acoustic survey results for capelin (Mallotus villosus) in Divisions 2J3K and 3LNO, 1980. NAFO SCR Doc. 81/5, Ser.No. N269, 10 p.

Miller, D.S., J.E. Carscadden and B. Bennett. 1978. An acoustic estimate of capelin (Mallotus villosus) biomass, ICNAF Divisions 2J and 3K, October and November 1977. ICNAF Res.Doc. 78/43 (Rev.), Ser.No. 5205, 7 p.

Miller, D.S., B.S. Nakashima and J.E. Carscadden. 1982. Capelin acoustic surveys in NAFO Divisions 2J + 3K, 3LNO, and 3L, 1981-82. NAFO SCR Doc. 82/54, Ser.No. N547, 12 p.

Mitchell, E. 1975. Trophic relationships and competition for food in Northwest Atlantic whales. Proc.Can.Soc.Zool., 2-5 June 1974, p. 123-132.

Nakken, O. and K. Olsen. 1977. Target strength measurements of fish. Symposium on Hydro-acoustics in fisheries research. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 170:52-69.

Pitt, T.K. 1958a. Distribution, spawning and racial studies of the capelin, Mallotus villosus Müeller) in the offshore Newfoundland area. J.Fish.Res.Board Can. 15:275-293.

__________. 1958b. Age and growth of the capelin. Mallotus villosus (Müeller) in the offshore Newfoundland area. J.Fish.Res.Board Can. 15:295-311.

__________. 1973. Food of American plaice (Hippoglossoides platessoides) from the Grand Bank, Newfoundland. J.Fish.Res.Board Can. 30:1261-1273.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res.Bull. 9:65-74.

Reddin, D.G. and J.E. Carscadden. 1981. Salmon-capelin interactions. CAFSAC Res.Doc. 81/2, 38 p.

Seliverstov, A.S. and S.M. Kovalev. 1976. Size of the capelin spawning stock on the Grand Newfoundland Bank. ICNAF Res.Doc. 76/51, Ser.No. 3837, 14 p.

Seliverstov, A.S. and L.I.Serebrov. 1979. Status of capelin stocks in Divisions 2J and 3K in 1978. ICNAF Res.Doc. 79/30. Ser.No. 5356, 12 p.

Serebrov, L.I., V.S. Bakanev and S.M. Kovalev. 1975. The state of the Newfoundland capelin stock. ICNAF Res.Doc. 75/7, Ser.No. 3435, 11 p.

Sergeant, D.E. 1963. Minke whales, *Balaenoptera acustorostrata* Lacepede, of western North Atlantic. J.Fish.Res.Board Can. 20:1489-1504.

____________. 1973. Feeding, growth and productivity of Northwest Atlantic seals. J.Fish.Res. Board Can. 30:17-29.

Sharp, J.C., K.W. Able, W.C. Leggett and J.E. Carscadden. 1978. Utility of meristics and morphometric characters for identification of capelin (*Mallotus villosus*) stocks in Canadian Atlantic waters. J.Fish.Res.Board Can. 35:124-130.

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus*) Müeller in Newfoundland waters. Nfld.Govt.Lab.Bull. 17:151 p.

____________. 1968. Review of some aspects of capelin biology in the Canadian area of the northwest Atlantic. Rapp.P.-v.Réun.Cons.int.Explor.Mer, 158:41-53.

Tuck, L.M. 1960. The murres: their distribution, populations and biology. A study of the genus *Uria*. Can.Wildl.Ser., Monogr.Ser. 1:206 p.

Vesin, J.-P., W.C. Leggett and K.W. Able. 1981. Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western Gulf of St. Lawrence and its multispecies implications. Can.J.Fish.Aquat. Sci. 38:257-267.

Winters, G.H. 1966. Contribution to the life history of the capelin, *Mallotus villosus*, in Newfoundland waters. Fish.Res.Board Can. MS Rep.Ser. No. 870. 56 p.

____________. 1970a. Record size and age of Atlantic capelin, *Mallotus villosus*. J.Fish.Res.Board Can. 27:393-394.

____________. 1970b. Biological changes in coastal capelin from the overwintering to the spawning condition. J.Fish.Res.Board Can. 27:2215-2224.

____________. 1974a. Rationale for partition of capelin quota in Subareas 2 and 3. ICNAF Res.Doc. 74/12, Ser.No. 3158, 2 p.

____________. 1974b. Back-calculation of the growth of capelin (*Mallotus villosus*) in the Newfoundland area. ICNAF Res.Doc. 74/7, Ser.No. 3150, 16 p.

____________. 1975. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res.Doc. 75/2, Ser.No. 3430, 25 p.

Winters, G.H. and J.E. Carscadden. 1978. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res.Bull. 13:21-30.

HERRING AND SPRAT: FISHERY INDEPENDENT VARIATIONS IN ABUNDANCE

by

Armin Lindquist

Director
Fishery Resources and Environment Division
Fisheries Department
FAO, Via delle Terme di Caracalla
00100 Rome, Italy

Resumen

Por lo menos a partir del siglo XVI han habido varios "períodos de arenque" que han sido de gran importancia socioeconómica para la provincia de Bohulän, en la costa de Skagerrak de Suecia. Durante estos períodos de arenque, el arenque entró en los confines del archipiélago cada invierno y fue pescado con redes de cerco de playa y redes agalleras. Capturas del orden de las 200 000 toneladas en una temporada de invierno eran usuales y al término de cada período - después que el arenque había estado entrando al archipiélago cada invierno por 20 a 50 años- la economía de la provincia declinó a niveles de pobreza.

Hay registros de la pesquería de espadín sólo para los últimos 100 años y durante ese tiempo se han observado cambios característicos en su distribución geográfica dentro del archipiélago, pero ninguna periodicidad.

La pesquería períodica de arenque y la pesquería de espadín estan relacionadas entre sí, sin embargo la pesquería de arenque está basada en clases anuales muy grandes de arenque del Mar del Norte, mientras que el espadín depende de condiciones hidrógraficas del Mar especiales. Estas condiciones hidrográficas son a su tiempo un prerequisito para que el arenque entre al archipiélago en grandes cantidades durante los períodos de arenque. Se hace referencia al trabajo por el cual el tipo de arenque fue identificado así como al posible mecanismo hidrográfico que afecta tanto al espadín como al arenque. Se sugiere que un debilitamiento de los vientos del oeste y un cambio en el flujo del Báltico hayan sido las claves de este fenómeno.

Se asume de que la secuencia de varios años en que clases anuales fuertes de arenque de Mar del Norte entraron al archipiélago son una expresión de la periodicidad que ocurrió en un área más amplia, pero no fue detectada debido a que no había pesquería de arenque en el mar abierto.

Para que ocurra el fenómeno conocido como "período de arenque" en el archipiélago de Bohuslän hay dos prerequisitos, que ocurren independientemente se requiere una secuencia larga de clases anuales fuertes y un cambio en el sistema general de circulación océanica. Esto implica que cuando no hay cambios en la circulación océanica pero clases anuales fuertes, el arenque no entra al archipiélago. Esto significa que la periodicidad mostrada por la pesquería de Bohulän no dará una imagén verdadera de la historia de las clases anuales fuertes del arenque del Mar del Norte.

INTRODUCTION

The discussion whether under natural conditions there is an equilibrium situation, permitting predictable yields, has been dominated by theoretical considerations. There are, unfortunately, not so many long-term series which monitor pelagic fish stocks. There are still less examples when human, i.e. fishery, influence can be considered negligible at least at the beginning and during the peak of the fishery. Fishermen know very well that availability of fish varies from year to year, but it has been difficult for them in discussions to distinguish between occurrences of fish in catchable quantities from stock sizes. As a matter of fact, this question is of little importance to the daily work of the fisherman. For the biologist it is of paramount importance - unfortunately the relation between fishability and stock size remains obscure and fishermen's observations can only be used with care. It therefore would be interesting to have examples with great natural fluctuations, which are well documented. One of the few cases where this has been possible is the case of the California sardine with the deposits of their scales in the sediment (Soutar and Isaacs 1974). It may be added that such work certainly should be carried out in other parts of the world and would give substantial information about natural fluctuations, such as those off Peru over the last 2 000 to 2 700 years (DeVries and Pearcy 1982).

One example of long-term fluctuations, which have been of greatest socio-economic importance are the herring periods in the Bohuslän archipelago, on the west coast of Sweden, Fig. 1. This fishery, in which the periodic appearance of herring has been mentioned since mediaeval times, has been studied more scientifically for the first time about one hundred years ago (Ljungman 1879). Many explanations have been given for the reason why the herring occurred in great masses, some of them of a highly speculative character (as periodicity in tidal waters caused by variations in frequency of sun spots). The only detailed investigations on the herring population(s) which gave rise to the periods has been made by Höglund (1972, 1978). The reason why the herring entered the archipelago *en masse* during the autumn and remained there during the winter has not however been explained. Other studies in the same area have shown that another clupeid changed its distribution and that this is likely to be connected with some hydrographic change (Lindquist 1964, 1978). The purpose of this contribution is to analyse further the phenomenon of the herring periods and to show that there are at least two independent mechanisms which may cause a herring period. Detailed observations may thus give pieces of a large puzzle but not necessarily predictable fluctuations.

THE PHENOMENON

Herring is recorded to have occurred in great quantities and be fished during long periods in the Bohuslän archipelago. These long periods, called herring periods, were interrupted by even longer periods when there was no herring and no fishery. Before this century there is no information whatsoever on the occurrence of herring in the open sea of the Skagerrak, as there was no herring fishery. It is well documented that the herring fishery in some of the "periods" had been of an extraordinary socio-economic importance for this province (Holmberg, 1963) which besides a moderate agriculture and some shipping had few other opportunities for earnings. The details of the herring periods have first been described by biologists and then by historians (for ref. see Höglund, 1976). According to the latter there are the following periods for which sufficient documentation is available, showing the economic problems following both the upswing when the herring appeared and the downswings when the herring ceased to enter the archipelago during the autumn and winter:

Herring in the archipelago	1556-89	(1643-1698 ?)	1747-1808/9	1877-1906	(no herring "period" since 1906)		
Herring in the open sea	-------------------- (no information) --------------------				-1920	1943-54	1963-65

The "period" in the seventeenth century is very questionable; Ljungman (1879) found that there was an abundant fishery at least between 1660 and 1680. For the latest period annual catches are given in Fig. 2. They are, considering the short coastal area and the gear used (see below) remarkable. During the season 1895-96 more than 200 000 t were caught. Still more remarkable are the catches in the period of the eighteenth century where catches were higher and amounted to about 270 000 t in one season, taken with beach seines only (Höglund 1976).

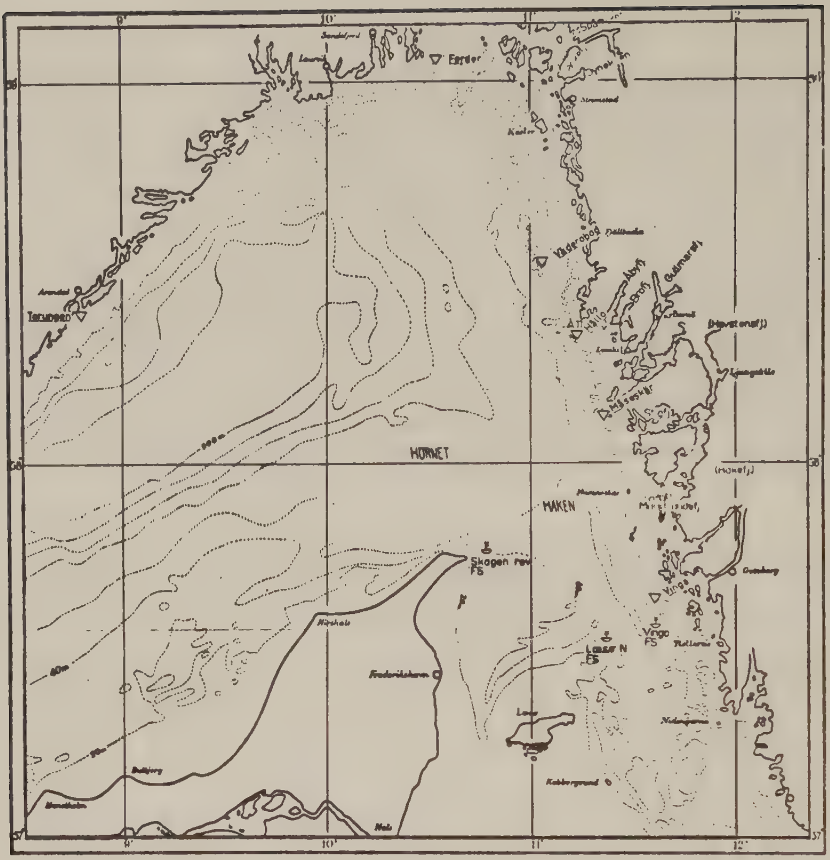

8°
10°
11°
12°
58°
57°
Færder
Strømstad
Koster
Väderöbod
Arendal
Torungen
HURNET
MAKEN
Skagen rev
FS
Vinga
FS
Læsø
Hirtshals
Frederikshavn
Göteborg
Bulbjerg
Hanstholm

Fig. 1. The area investigated: (northern) Kattegat, Skagerrak.

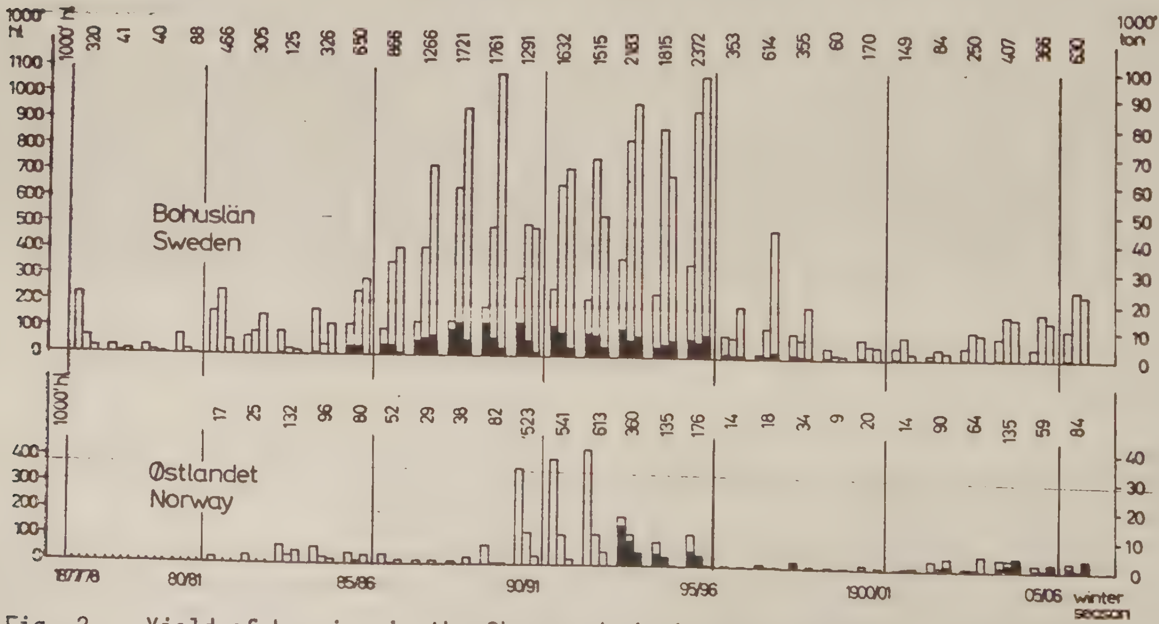


Fig. 2 . Yield of herring in the Skagerrak during the winters of 1877/1878 to 1906/1907.

Earlier periods have been claimed to have taken place but a closer look shows that those periods do not stand the examination of the professional historians. For those earlier "periods" there are only scattered reports in mediaeval documents or in the sagas. The periods given above are thus those which we can accept as facts. Herring was so abundant that it was fished with gillnets and beach seines and only from the very end of the last century with purse seines.

For the time from 1903 onwards there is additional information with biological data, Hoglund and earlier authors (as Andersson, for reference see Höglund, 1979) have pointed out that the same herring as in the archipelago occurred during the winter in the open Skagerrak and they found years of abundant appearance, calling them "open sea herring periods". As the open sea fishery started in 1903 and ceased in 1920 this is considered as being the real end of the herring period which started in 1877. There were two later periods with great herring abundance and a rich fishery in the open Skagerrak, but not in the confines of the archipelago, namely 1943-1954 and 1963-1965.

The time until 1920 with the fishery in the open sea is considered to be simply a continuation of the herring period within the archipelago - but at the end the herring for some reason did not enter the confines of the archipelago any more. The other "open sea" periods occurred independently from any invasion into the archipelago. Similar open sea periods during the winter in the Skagerrak may have occurred earlier between the recorded herring periods, without having been noticed as there was no fishery in the open sea.

Of the about 10-30 fish species of economic importance occurring in the area, only three are pelagic, namely apart from herring, sprat (Sprattus sprattus) and mackerel (Scomber scombrus). The latter is a seasonal immigrant during the warmest time of the year and is of little interest in this connection. For the former there are observations available for the fishery during the last hundred years (Lindquist 1978). Sprat occurs in shoals, either nearly devoid from herring or mixed with small herring of the same size. Before about 1970 sprat was only fished for human consumption and sales resulted in high prices. The main fishery in the Skagerrak was carried out during the winter in the confines of the archipelago and observations on quantities and localities of the fishery exist since 1860 (Lindquist 1964). From the analysis of the records it can be seen that the location of the fishery has changed several times between the northern and southern part of the coast, Fig. 3. As sprat fishermen always followed the sprat on its move one can be fairly sure that the location of the fishery reflected occurrence. As regards quantities fished and landed, there has not been any kind of "regularity" as in the herring fishery.

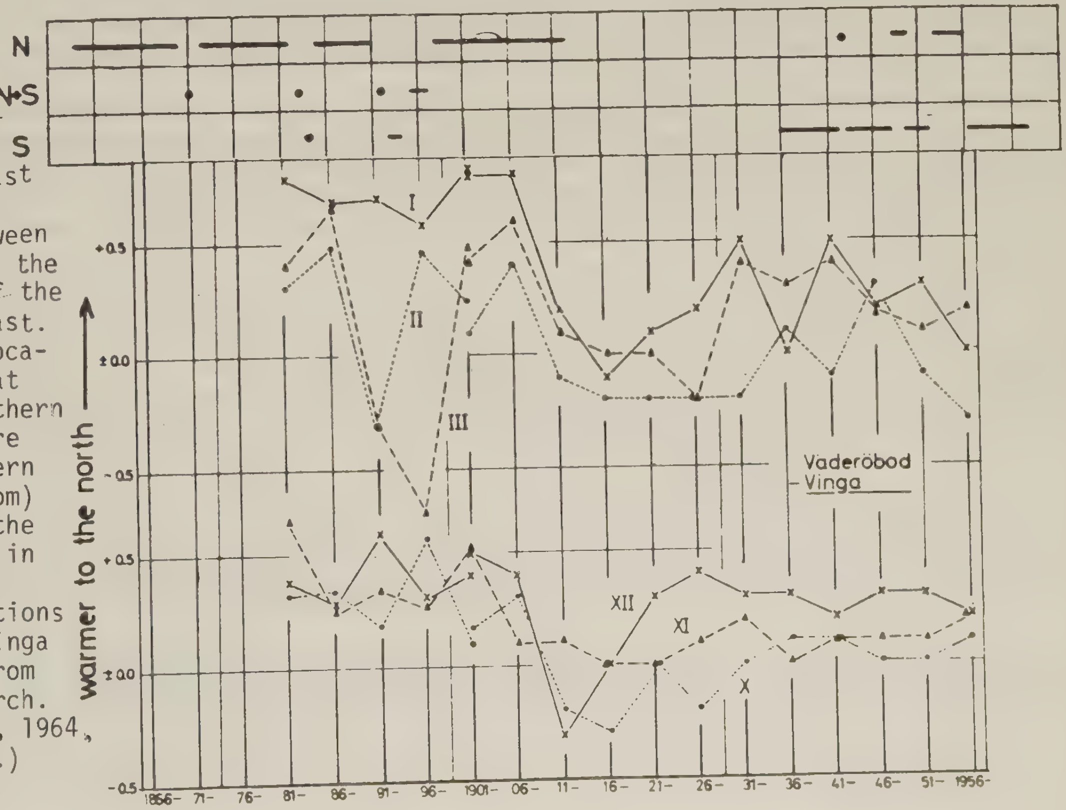


Fig. 3. Location of the sprat fishery off the Swedish west coast and temperature differences between the northern and the southern part of the Swedish west coast. (a, top) Main location of the sprat fishery: N, northern part; N+S, entire coast; S, southern part. (b, bottom) Differences in the air temperature in 5-year periods between the stations Väderöbod and Vinga (see Fig. 1), from September to March. (From Lindquist, 1964, partly modified.)

BIOLOGICAL BACKGROUND

Unfortunately there are rather few length measurements and age determinations of the herring which formed the bulk of the last herring period, thus not allowing for a reliable identification of all the herring. Indirect methods showed that it is very likely that it was the autumn spawning North Sea herring (NSAS) which wintered in the confines of the archipelago of Bohuslän. For the open sea period which ended in 1920 and the later open sea periods it has been shown to be NSAS. For the herring period 1747-1808/9 there is a rich material of remnants of train oil factories, as the train oil waste was buried ashore, where it still can be found in many places. Höglund investigated those semi-fossil layers consisting of vertebrae and other bones (scales disappear during the cooking process) and found that the age composition, length/ distribution, and annual ring pattern of the majority of the herring caught some 200 years ago and used for production of train oil is similar, if not identical, with the herring fished now in of the North Sea (including the Skagerrak and the Kattegat).

It can therefore safely be assumed that the herring during any of the herring periods was of the same type.

For sprat no races of the kind found in herring have been described and no meristic or morphometric groupings of sprat from the coastal fishery in the Skagerrak have been found (see further Lindquist 1968).

HYDROGRAPHICAL BACKGROUND

There are few long-term hydographical series in the Skagerrak, and those existing permit only calculations of mean temperatures. Frogner (1948) showed that there has been a substantial increase in mean temperatures in spring to autumn temperatures since the thirties (stations Torungen and Flødevigen on the Norwegian Skagerrak coast), Fig. 4. There is no tendency or any event in the temperature regime which can be connected with the onset or end of the last herring period. Lamb (1973) has shown how the intensity of westerly circulation over the British Isles changes since 1860, Fig. 5.

In order to get longer time series another approach was made, using air temperatures in the coastal area, as it has been observed that there is a firm relationship between air temperature and sea surface temperature (Frogner, 1948). Lindquist (1964) showed that even when using this method there is no direct relation between mean temperatures and the latest herring period, 1877-1906.

The picture becomes quite different, however, if for one hundred years annual temperature differences are compared between the northern and the southern Skagerrak, not absolute values of surface temperature, Figs. 3 and 6. It was found that the northern coast during the long time of observations has been either warmer or colder as compared to the southern coast, the border between "north" and "south" seems to be in the middle, where there is a boundary area of different water masses, known to fishermen.

This hydrographical background fits rather neatly with the localization of the sprat fishery, Fig. 3. As sprat is a relatively warm water fish, sprat follows or at least is found in areas which are warmest during autumn/winter. Sprat was thus found either in the northern part or in the southern part of the coast during the last one hundred years. This seems reasonable as a fish cannot compare a mean value now with that from last year or earlier. Therefore gradients only are of importance. They allow for preferences within physiological limits.

From the same hydrographic material another observation can be made: the latest herring period at the turn of the century coincides well with the time when the northern coast was warmer during winter. This also coincides with the time when the westerly winds were weaker, Fig. 5, and the colder Baltic water from the south would have gained a wider distribution.

As herring is a cold water fish a simple explanation of temperature preference as in the case of sprat cannot be given. The picture, however, may be much more complicated as the changed temperature regime may be the expression of larger hydrographic changes which are as yet unknown.

Even from this century (in the forties) there are minor trends in differences in surface temperature making it likely that there have been similar hydrographical changes as earlier.

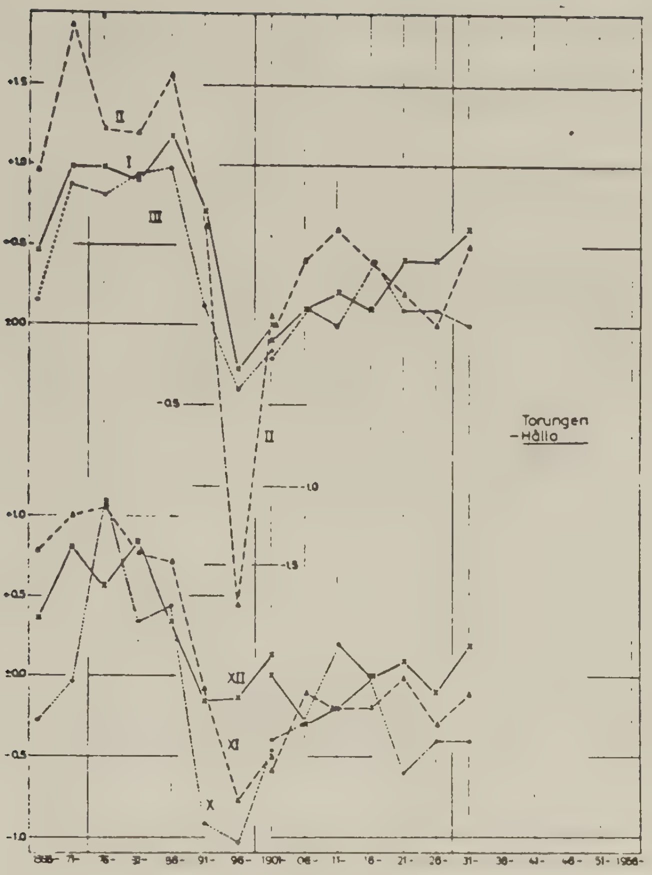


Fig. 4. Differences between the air temperature in 5 years periods at the stations Torungen and Hallo, each month X - III.

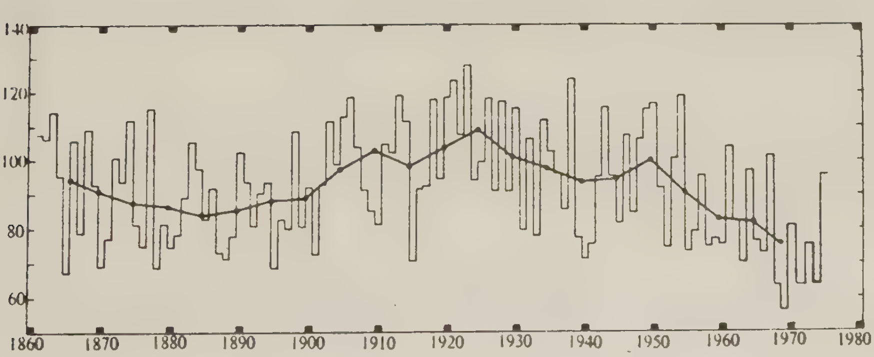


Fig. 5. Number of days per year of general westerly circulation over the British Isles (Lamb, 1973).

HYPOTHESIS

From the studies referred to above one can draw the following conclusions:

- the fluctuations in the quantity of herring must basically have been caused by a sequence of strong year classes of mainly North Sea herring; and
- there has been a hydrographic event of a nature not known in detail occurring at the time of the last herring period.

A series of good year classes has to be assumed as the herring periods lasted for two to five decades with the herring arriving nearly every autumn/winter in the archipelago. The material from the two last herring periods shows that the majority of herring belongs to North Sea herring. When a sequence of good year classes is terminated, the stock gets more vulnerable to the fishery thus accelerating the end of the herring period. The total catches of herring in the North Sea are recorded since the beginning of this century and do not show any tendency which can be related to the Skagerrak situation (Burd 1978, Fig. 128, 132). Earlier statistics apparently do not exist.

The reason why the herring entered the confines of the archipelago *en masse* every autumn is unknown but is most likely connected with changes in current systems and in the outflow from the Baltic Sea.

We find thus two different mechanisms, the biological one and the hydrographical one, the latter given one of the necessary conditions for the phenomenon of a herring period in the archipelago. When there are both strong year classes and the necessary hydrographic conditions, herring appeared in the archipelago. There remains now the question of why both the sequence of good year classes and the hydrographical changes happen at the same time. This question is, however, not strictly justified, as there may have been other "periods" i.e., sequences of good year classes which were never detected because the hydrographic conditions at the most prevented or at least did not favour entering the confines of the archipelago. It is possible that both a sequence of good year classes and hydrographical changes are expressions of larger changes (westerlies) and may have the same ultimate cause, but this has to be left as an open question.

The important conclusions are (a) that the North Sea herring as such must have shown a periodicity not observed elsewhere; and (b) that temperature differences have been of greater importance for the distribution of fish and the fishery than absolute temperatures.

SUMMARY

1. The Bohuslan herring periods are caused by a sequence of strong year classes of North Sea herring.
2. Before the present day situation this herring has been regularly wintering in the Skagerrak where it was fished since the beginning of this century. Entering the Bohuslan archipelago by the wintering herring is supposed to be the consequence of some long-term environmental change.
3. Local long-term environmental changes have only been observed in the differences in temperature between coastal areas, but not in absolute temperatures. Over the whole North Sea the intensity of westerly winds has changed and this may have caused the observed trends in temperature differences.
4. Within the physiological tolerance limits of the fish there may be preferences in a given situation, which will not be detected by mean absolute temperatures but only by means of differences in temperatures. The distribution of sprat during the last one hundred years can be explained by this. The latest herring period occurred when the northern coastal area was considerably warmer during the winter.
5. The periodic appearance of herring in the confines of the archipelago is supposed to have been caused by two independent mechanisms: firstly many strong year classes of herring, and secondly a major hydrographic change, favouring entering the confines of the archipelago and wintering there.

REFERENCES

Burd, A. 1978. Long-term changes in North Sea Herring Stocks. Rapp.P.-v.Réun.Cons.int.Explor. Mer. 172: 137-153.

DeVries, D.S. and W.G. Pearcy. 1982. Fish debris in sediments of the upwelling zone off Central Peru: a late Quaternary record. Deep-Sea Res. 28(1A):87-109.

Frogner, E. 1948. Means and extremes of sea temperature by the Norwegian coast. Geofys. Publ. 15(3): 82 p.

Höglund, H. 1972. On the Bohuslän herring during the great herring fishery period in the eighteenth century. Inst.Mar.Res. Lysekil, Ser.Biol. (20): 86 p.

____________. 1976. Bohusläns sillperioder. Medd. Havsfiskelaboratoriet, Lysekil. No. 207. 43 pp.

____________. 1978. Long-term variations in the Swedish herring fishery off Bohuslän and their relation to North Sea herring. Rapp. P.-v.Réun. Cons.int.Explor.Mer. 172:175-186.

Holmberg, A. 1963. Perioden 1550-1880. pp. 149-353. In Bohusläns Historia (Erik Lönnroth, ed.). Uppsala, Stockholm/Göteborg.

Lamb, H. 1973. Whither climate now. Nature, Lond. 244 (54/6):395-397.

Lindquist, A. 1964. Zur Fischereihydrographie der Sprotte (*Clupea sprattus*) an der schwedischen Westküste. Inst.Mar.Res.Lysekil, Ser.Biol. Rep.15, 87p.

____________. 1968. Meristic and morphometric characters, year-classes and "races" of the sprat (*Sprattus sprattus*). Inst.Mar.Res. Lysekil. Ser.Biol. Rep.17. 14 p.

____________. 1978. A century of observations on sprat in the Skagerrak and the Kattegat. Rapp. P.-v.Réun,Cons.int.Explor. Mer. 172: 187-196.

Ljungman, A.V. 1879. Bidrag till lösningen af frågan om de stora sillfiskenas sekulära periodicitet. Nord.Tidskr.f. Fiskeri: 257-268.

Soutar, A. and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment of the Californias. Fish.Bull. U.S. 72:257-273.

MONSOON-INDUCED SEASONALITY IN THE RECRUITMENT OF PHILIPPINE FISHES*

by

D. Pauly[1] and N.A. Navaluna[2]

[1]International Center for Living Aquatic Resources
Resources Management (ICLARM)
MCC P.O. Box 1501
Makati, Metro Manila
Philippines

[2]Institute of Fisheries Development and Research
College of Fisheries
University of the Philippines in the Visayas
Diliman, Quezon City
Philippines

* ICLARM Contribution No. 136

Resumen

Se han estudiado en detalle los patrones del reclutamiento de 112 stocks de peces teleósteos de Filipinas, los cuales provienen de 23 familias, 34 géneros y 57 especies. El patrón de reclutamiento anual generalmente muestra una estructura bimodal con dos picos de fuerza diferente, separados por cuatro y ocho meses. Los estimados del reclutamiento fueron obtenidos por una proyección hacia atrás de los datos de frecuencia de longitudes, basándose en datos de 900 mil medidas de longitud realizadas entre 1958 y 1981.

Se muestra que esta periodicidad corresponde al patrón estacional del viento de los monzones en las Filipinas.

INTRODUCTION

Elucidating the factors which determine *between* year fluctuations in recruitment is one of the major tasks presently facing fisheries research (Bakun et al., 1982). However, faced with the problem caused by a scarcity of data points, a number of workers have chosen to investigate *within* year fluctuations of recruitment in an attempt to identify factors which may affect reproductive success (see Johannes, 1978 for a review).

This paper is an investigation of the seasonality of recruitment of Philippine fishes based on the detailed analysis of a large body of length-frequency data using the computer programs ELEFAN I and II (Pauly and David, 1981; Pauly, 1982).

Pending a more detailed analysis, which will include a set of climatological and hydrological data, the general features of the recruitment patterns of Philippine fishes are presented here to allow comparisons with data obtained from areas with oceanographic and climatological regimes different from that of the Philippines.

The data presented here also allow for comparisons with inferences drawn earlier by other authors on the spawning and recruitment seasons of Philippine fishes. Concerning these earlier studies, it must be mentioned, however, that the conceptual difference between a *spawning* and a *recruitment* season had generally not been made, i.e., studies on gonadal maturation stages and analyses of length-frequency data were both used in inferences regarding "spawning seasons". In the present study, we report only on the periodicity of *recruitment*.

MATERIAL AND METHODS

The materials used for this paper consist of length-frequency data sets from approximately 0.9 million fish, collected by individual researchers and the staff of several agencies (foremost, the Bureau of Fisheries and Aquatic Resources) from 1958 to 1981 at various locations throughout the Philippines (Fig. 1). The data cover 112 stocks of teleostean fishes, ranging in size from gobies to tuna and covering 23 families, 34 genera and 57 species (Table 1). These raw data and their sources are fully documented in Ingles and Pauly (1982) and detailed analyses are given in Ingles and Pauly (in press).

Each length-frequency data set was analyzed in terms of growth using the ELEFAN I program of Pauly and David (1981). Applications of this method have been presented in a number of papers (Pauly and David, 1981; Pauly and Ingles, 1981; Pauly and Tsukayama, this volume) and the reader is referred to these for details on the method. The growth parameters L_∞ and K of the von Bertalanffy Growth Function (VBGF) extracted from the length-frequency data described above are given in Ingles and Pauly (1982).

Once growth parameters pertaining to a given stock have been extracted, they can be used to project the data backward onto the time axis such that the pattern of recruitment which generated the structure of the length-frequency data set can be reconstructed (Fig. 2). A computer program named ELEFAN II (Electronic LEngth Frequency ANalysis) which has the computation of recruitment pattern as one of its major routines (Pauly, 1982) was used for this purpose.

Recruitment patterns, as defined and computed by ELEFAN II have the following features:

a) Their exact position on the time axis is known only when t_0, the third parameter of the VBGF, is known. Since length-frequency data alone do not allow the estimation of t_0, the abscissa of recruitment patterns is not fixed in real time, and is therefore labelled "1 year" (see Fig. 2).

b) They always include one month with zero recruitment. This is due to the fact that when the projections of the length-frequency data onto the time axis is completed, the lowest of their 12 monthly values of apparent recruitment is subtracted from each of the 12 monthly values; this is

Table 1. Summary of data on the recruitment patterns of 112 fish stocks from Philippine waters. Stock numbers refer to classification in Ingles and Pauly 1982 and Ingles and Pauly, in press.[a]

#	Stock identification Species	% in smaller of two recruitment pulses[b]	Smaller time between two recruitment pulses (mo)[c]	Sample size
1	*Sardinella fimbriata*	43.7	5.1	1253
2	*Sardinella fimbriata*	26.0	4.3	166
3	*Sardinella longiceps*	30.8	4.6	1870
4	*Sardinella longiceps*	—	—	6191
5	*Sardinella melanura*	28.3	3.0	794
6	*Sardinella sirm*	—	—	211
7	*Stolephorus commersonii*	8.3	3.4	9422
8	*Stolephorus heterolobus*	19.5	5.4	2087
9	*Stolephorus heterolobus*	8.9	4.3	2345
10	*Stolephorus indicus*	37.7	2.7	3402
11	*Stolephorus indicus*	—	—	6514
12	*Stolephorus zollingeri*	6.5	4.3	29388
13	*Stolephorus zollingeri*	28.0	3.3	40864
14	*Stolephorus zollingeri*	10.6	4.2	6029
15	*Saurida tumbil*	18.0	4.7	4174
16	*Saurida tumbil*	21.5	5.4	589
17	*Saurida undosquamis*	—	—	26262
18	*Hemirhamphus georgii*	35.3	3.3	5098
19	*Ambassis gymnocephalus*	17.4	6.7	1477
20	*Epinephelus sexfasciatus*	32.1	4.5	738
21	*Therapon plumbeus*	31.8	4.3	1588
22	*Therapon theraps*	30.7	2.4	2014
23	*Priacanthus tayenus*	33.7	5.4	3672
24	*Sillago sihama*	13.7	2.8	4652
25	*Decapterus macrosoma*	33.3	5.8	3349
26	*Decapterus macrosoma*	9.0	3.5	9781
27	*Decapterus macrosoma*	28.2	2.7	4075
28	*Decapterus macrosoma*	75.2	3.2	25021
29	*Decapterus macrosoma*	26.9	1.8	13528
30	*Decapterus macrosoma*	10.9	2.2	34836
31	*Decapterus macrosoma*	11.2	2.8	8108
32	*Decapterus macrosoma*	5.3	5.8	625
33	*Decapterus macrosoma*	0.8	3.5	1949
34	*Decapterus macrosoma*	2.9	3.9	3079
35	*Decapterus macrosoma*	16.5	4.8	339
36	*Decapterus macrosoma*	35.5	3.0	16919
37	*Decapterus macrosoma*	3.0	4.5	11985
38	*Decapterus russelli*	6.0	4.1	13462
39	*Decapterus russelli*	5.8	4.4	7026
40	*Decapterus russelli*	5.9	4.2	11091
41	*Decapterus russelli*	2.0	4.1	7092
42	*Decapterus russelli*	14.7	3.8	9116
43	*Elagatis bipinnulatus*	—	—	128
44	*Selar crumenopthalmus*	17.8	5.3	2287
45	*Selaroides leptolepis*	20.8	5.0	4440
46	*Selaroides leptolepis*	13.3	4.1	1389
47	*Mene maculata*	1.2	5.1	2160
48	*Gazza minuta*	34.1	4.9	854
49	*Gazza minuta*	14.8	3.4	511
50	*Leiognathus bindus*	16.1	4.7	6286
51	*Leiognathus bindus*	31.6	4.8	2074
52	*Leiognathus bindus*	1.7	4.0	1002
53	*Leiognathus blochii*	5.6	5.3	615
54	*Leiognathus blochii*	16.8	4.3	1401
55	*Leiognathus blochii*	48.2	2.8	931
56	*Leiognathus blochii*	20.6	3.6	936
57	*Leiognathus brevirostris*	28.7	4.3	29669
58	*Leiognathus daura*	—	—	4074
59	*Leiognathus daura*	3.7	5.2	6140
60	*Leiognathus daura*	3.7	4.1	1301

Table 1 (Cont.)

#	Stock identification Species	% in smaller of two recruitment pulses[b]	Smaller time between two recruitment pulses (mo)[c]	Sample size
61	*Leiognathus equulus*	45.4	5.0	9660
62	*Leiognathus leuciscus*	18.7	4.0	1754
63	*Leiognathus leuciscus*	—	—	1872
64	*Leiognathus lineolatus*	3.4	4.5	1530
65	*Leiognathus lineolatus*	3.3	3.3	3326
66	*Leiognathus lineolatus*	5.0	3.6	1685
67	*Leiognathus splendens*	7.3	4.9	58090
68	*Leiognathus splendens*	17.6	2.9	67005
69	*Leiognathus splendens*	1.5	4.1	33879
70	*Leiognathus splendens*	7.6	5.3	95253
71	*Secutor insidiator*	38.2	3.9	3835
72	*Secutor insidiator*	—	—	1253
73	*Secutor insidiator*	—	—	181
74	*Secutor ruconius*	18.7	5.0	38051
75	*Secutor ruconius*	34.8	3.3	10217
76	*Secutor ruconius*	6.5	4.3	1820
77	*Nemipterus japonicus*	37.4	4.7	3665
78	*Nemipterus nematophorus*	29.2	3.6	1290
79	*Nemipterus nematophorus*	10.5	4.2	1477
80	*Nemipterus ovenii*	35.3	4.2	3276
81	*Pentaprion longimanus*	—	—	6174
82	*Pentaprion longimanus*	45.3	4.6	3454
83	*Pomadasys argyreus*	—	—	2014
84	*Pomadasys argyreus*	4.6	4.9	18476
85	*Pomadasys argyreus*	25.0	3.5	15217
86	*Pomadasys argyreus*	25.3	3.2	7727
87	*Dendrophysa russelli*	24.2	3.9	779
88	*Otolithes ruber*	49.9	3.4	1444
89	*Otolithes ruber*	44.2	4.2	1629
90	*Pennahia anea*	28.3	3.1	4354
91	*Pennahia macropthalmus*	20.0	4.0	498
92	*Upeneus moluccensis*	19.2	5.3	8594
93	*Upeneus sulphureus*	30.5	4.8	48547
94	*Upeneus sulphureus*	14.6	4.0	787
95	*Upeneus vittatus*	10.1	5.0	3816
96	*Scatophagus argus*	18.1	5.3	1977
97	*Liza subviridis*	44.9	4.3	6104
98	*Glossogobius giurus*	16.5	2.8	2191
99	*Glossogobius giurus*	16.3	3.5	1577
100	*Trichiurus lepturus*	8.5	3.6	3711
101	*Trichiurus lepturus*	22.7	2.7	3128
102	*Trichiurus lepturus*	19.0	4.1	11993
103	*Auxis thazzard*	27.9	6.2	1518
104	*Auxis thazzard*	42.4	2.5	1048
105	*Katsuwonus pelamis*	7.4	3.7	1118
106	*Katsuwonus pelamis*	—	—	1908
107	*Rastrelliger brachysoma*	17.8	4.2	2966
108	*Rastrelliger brachysoma*	23.3	5.5	2970
109	*Rastrelliger kanagurta*	6.9	3.1	431
110	*Scomberomorus commerson*	43.2	5.6	444
111	*Thunnus albacares*	5.2	4.5	813
112	*Cynoglossus puncticeps*	45.3	3.6	2571
		$\bar{X}$ = 20.2 %	$\bar{X}$ = 4.1 months	Σ = 894119
		S.E. = 1.33 %	S.E. = 0.09 month	

---

[a] Dashes refer to recruitment patterns which could not be separated into two component distributions (see *K. pelamis* in Fig. 3 for an example).

[b] Percent of recruits in larger pulse = 100 — % in smaller pulse.

[c] Larger time (in months) between two pulses = 12 — smaller time between two pulses.

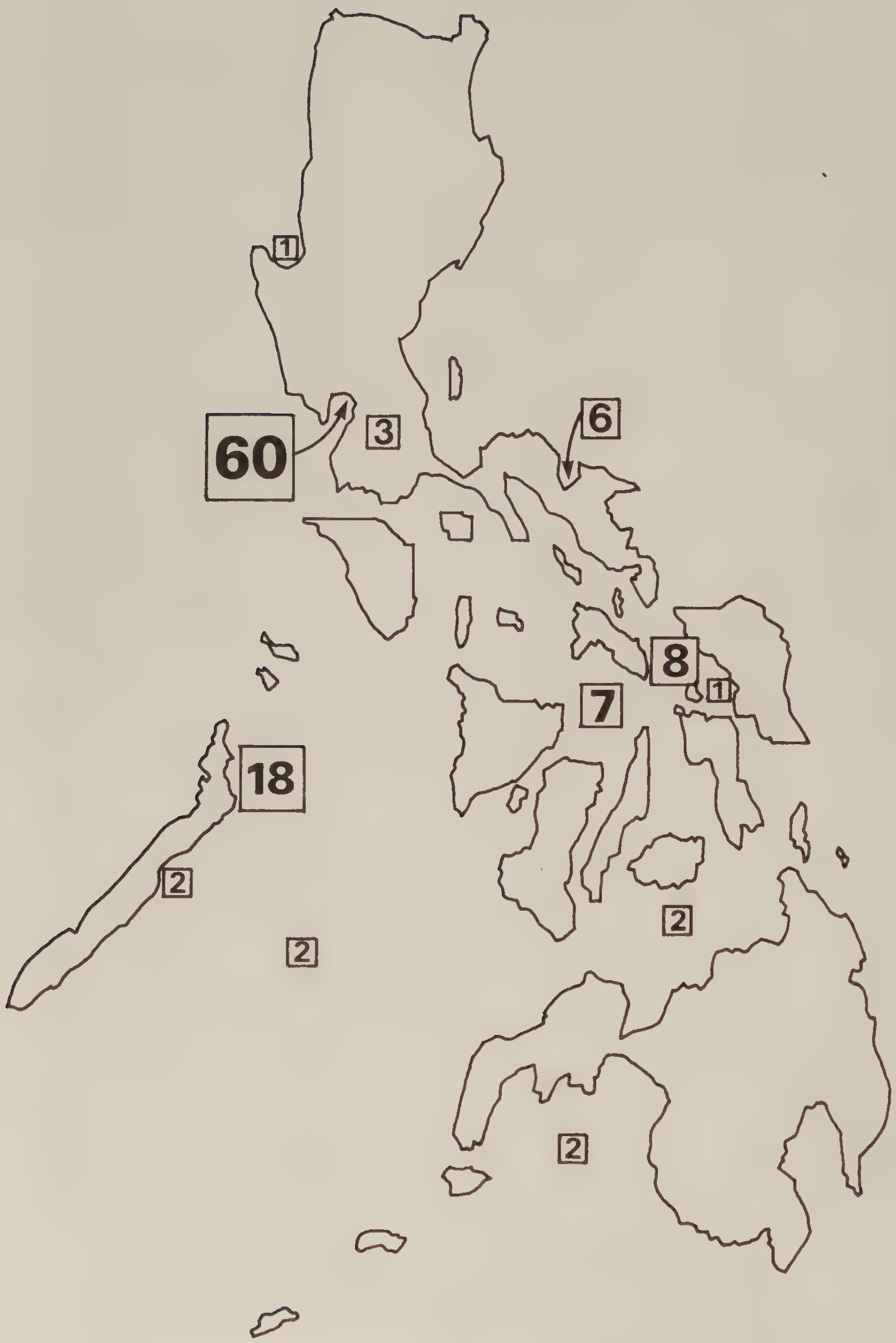


Fig. 1 Sampling location of length-frequency data discussed in this paper; the numbers refer to the number of stocks from each locality (total 112, see also Table 1).

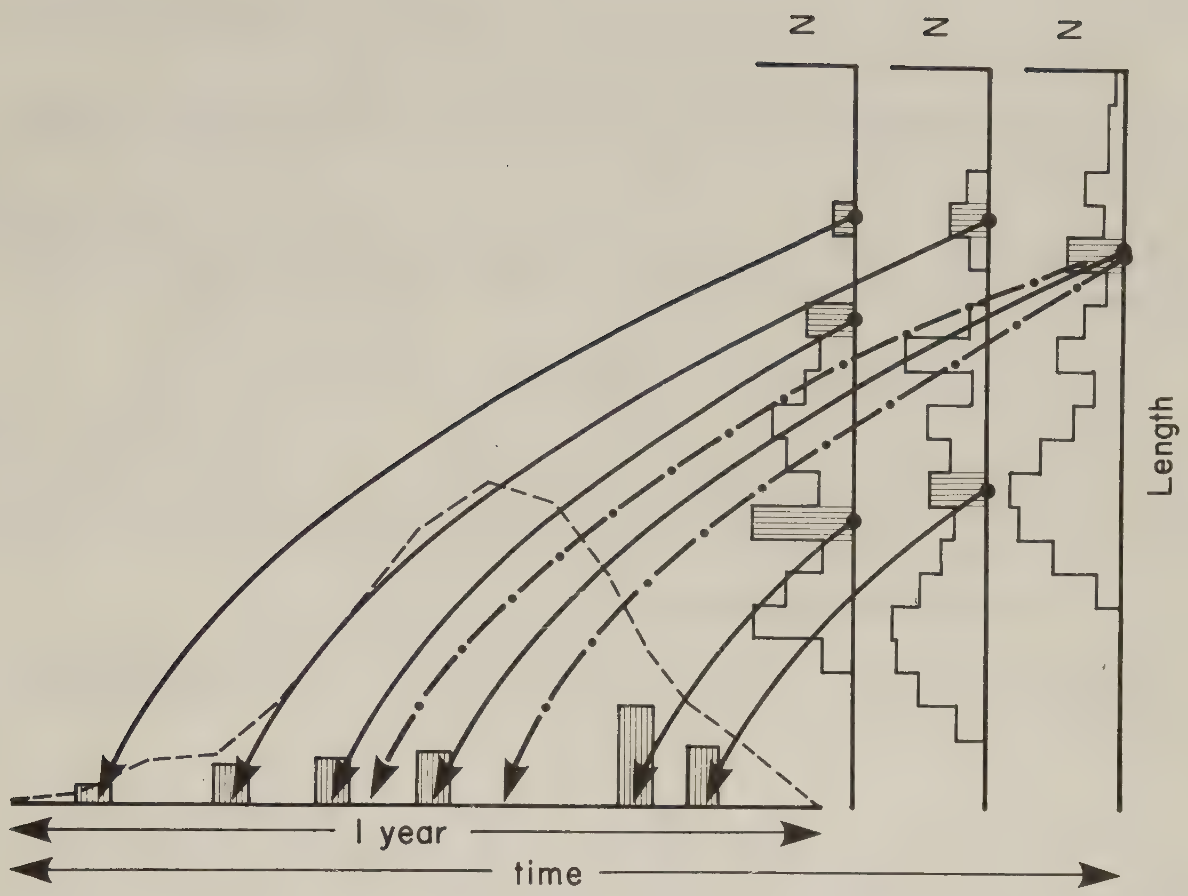


Fig. 2 Schematic representation of method for obtaining recruitment patterns using ELEFAN II. The steps involved are: 1) projection onto the time axis of the frequencies of a set of length-frequency data; 2) summation for each month of the frequencies projected onto given months (the dotted line gives the sums achieved for each month after the projection of frequencies suggested by the arrows is completed); 3) subtraction, from each monthly sum of the lowest of the 12 monthly sum, to obtain a zero value where apparent recruitment was lowest; 4) output of monthly apparent recruitment, in % of annual recruitment. The projection of only a few (shaded) frequencies is shown here. In reality, all frequencies are projected, resulting eventually in the superimposed recruitment pattern (dashed line). Note "blurring" effect of individual growth curves (—•—•—) differing from the mean growth curve of the stock (solid lines; also note that t_0 is here assumed equal to zero, see text). (Adapted from Pauly _et_ _al_., 1981).

done to reduce the "noise" due to fish having grown in a fashion different from that predicted by the growth parameters used (see Fig. 2).

Pauly (1982) showed how recruitment patterns, as obtained from ELEFAN II, can be used to objectively distinguish fish with one marked recruitment season from fish with two such seasons per year.

In this paper, we have carried this analysis one step further, and used the NORMSEP program of Abrahamson (1971)* to separate the recruitment patterns into normally distributed components. This analysis provided the following information for each recruitment pattern:

- number of normally distributed component distributions (number of recruitment pulses per year)
- standard deviation (s.d.) of each component distribution (the s.d. is proportional to the duration of a recruitment pulse)
- time (in months) separating different recruitment pulses
- proportion of recruits in the component distributions.

Fig. 3 gives examples of recruitment patterns separated into their component distributions.

RESULTS

Of the 112 recruitment patterns examined, only 12 did not consist of two major components (Table 1). The 100 recruitment patterns which separated readily into two component distributions had maxima which were, on the average 4.1 and 7.9 months apart. On the average, the major recruitment pulse of these 100 recruitment patterns contained 80% of the annual recruitment, while the minor pulse contained the remaining 20%.

In the case of five groups of fish, the results obtained here can be compared with inferences on recruitment and spawning seasons drawn earlier by other authors from analyses of length-frequency data (inference on recruitment) and studies of gonadal maturation stages (inferences on spawning). These five groups are as follows:

- *Stolephorus* spp.: Tiews et al. (1975b) concluded the following on the spawning of anchovies: "although *S. heterolobus* [...] breeds throughout the year, a peak spawning was noted during the northeast monsoon season (October to March)[...]. This can be distinguished from a period of little or no spawning activity from April to July. The findings for *S. bucaneeri* are similar [...]. However, it is probable that the spawning time begins earlier in June and does not extend to February. No spawning was observed in March, April and May." In the case of *S. indicus*, Tiews et al. (1975b) suggest that it spawns and recruits over the major part of the year.

  Our results, on the other hand, showed that recruitment of the stolephorid anchovies, conform to the typical bimodal pattern presented above (see Table 1).

- *Saurida tumbil* (Synodontidae): Tiews et al. (1972) found that "the *S. tumbil* population in Manila Bay and adjacent waters had a protracted breeding period and spawns two or even three times a year in a quite irregular manner." Our results, based on data from the Visayan Sea and from Manila Bay, show that *S. tumbil* recruits twice a year (Table 1).

---

*The version of NORMSEP we used is a translation into BASIC of the (FORTRAN) original; it was prepared by Mr. N. David. The program which was run on a Radio Shack TRS 80 Model III microcomputer is available from D. Pauly, ICLARM.

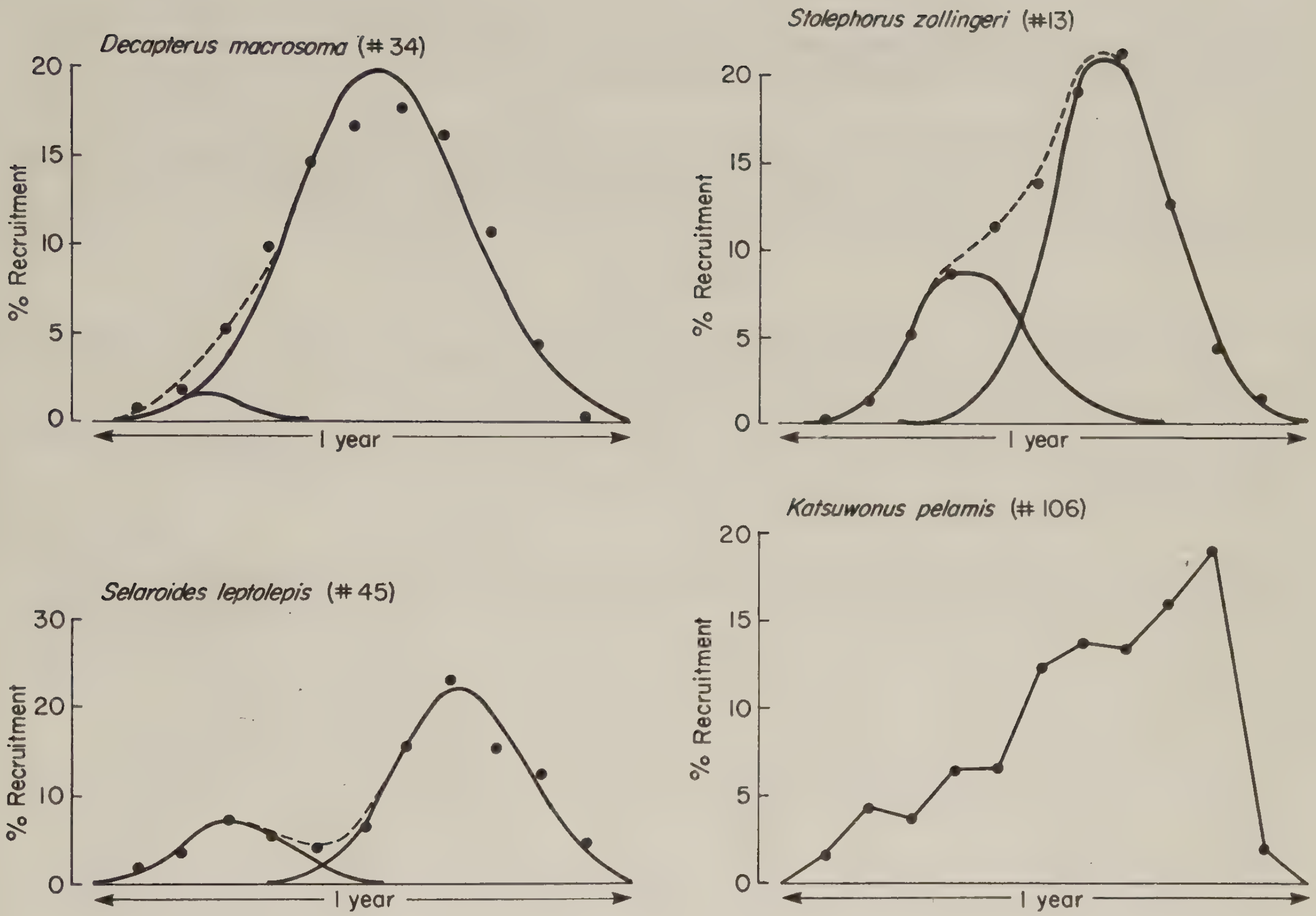


Fig. 3 Examples of recruitment patterns separated into their component distributions (dotted line obtained by combining two normal distributions). Note difficulty in deciding in cases such as that of *D. macrosoma* whether there are one or two recruitment pulses; also note good separations in two other cases, one with wide overlap (*S. zollingeri*), the other with little overlap (*S. leptolepis*). Last case (*K. pelamis*) is that of a stock where separation into a small number of components is not feasible. More details on 3 of these 4 cases are given in Table 1.

- *Decapterus* spp. (*D. macrosoma* and *D. russelli*): Tiews et al. (1975a) "concluded that the breeding period of both species extends from November to March in Palawan Waters [and that] spawning time seemed to be delayed by 1-2 months, thus extending to April and May."

  Our results suggest either one single, protracted recruitment season or two recruitment seasons, one much shorter than the other (Table 1).

- *Rastrelliger brachysoma*: Tan (1970) concluded that "spawning occurs from June to February" in Manila Bay. Our analysis of length-frequency data on this fish, collected in the Samar Sea, suggests that *R. brachysoma* is recruited twice a year, and follows the general pattern outlined above.

DISCUSSION

Although it is generally agreed that the *spawning* seasons of tropical fishes are generally longer than those of their temperate counterparts (Johannes, 1978), the demonstration is lacking that this also generally applies to their *recruitment* seasons. Thus, it could be that the eggs produced during a long spawning season generally encounter a "survival window" (Bakun et al., 1982) that is open during a short period only, resulting in sharply peaked recruitment pulses (Munro, in press).

This problem cannot be resolved at present because recruitment patterns (as defined here) from temperate fishes are not available for comparison. The data at hand allow, however, for the generalization that Philippine neritic fishes have pulses of recruitment twice a year - as opposed to their temperate counterparts which generally recruit once a year.

The two recruitment pulses that seem to be typical of Philippine fishes are of unequal strength, and their asymmetry is emphasized by the feature that, rather than dividing the year in two equal halves of 6 months each, the two recruitment pulses divide the year into two periods of unequal duration of about 4 and 8 months. This periodicity is close to the 5- and 7-month rhythm of the monsoon winds which, in the Philippines, blow from the northeast from September to March with peaks from November to January (northeast monsoon), then blow from the southwest from April to August with peaks in May-June (southwest monsoon) (Dickerson, 1928, p. 39).

This study thus supports the hypothesis of a relationship between spawning/recruitment patterns and monsoon winds, as suggested by Weber (1976) and Johannes (1978) for various areas of the tropical Indo-Pacific, including the Philippines.

Winds generally determine the extent of both horizontal advection and therefore upwelling events and vertical instability, which, as hypothesized in Bakun and Parrish (1981), may have crucial effects on the survival of fish larvae (see also Bakun et al., 1982).

Highly aggregated data such as those presented here do not allow testing of these and related hypotheses directly. However, the generalization presented here that the recruitment patterns of Philippine fishes match the monsoon wind patterns can be tested on a finer scale. We plan to compare single recruitment patterns pertaining to a given stock in a given year and place with the wind patterns (and the patterns of wind-driven phenomena such as upwellings and turbulence) prevailing when and where recruitment occurred. These tests may help establish in more detail the link between wind-driven oceanographic phenomena and increased larval survival in tropical areas such as the Philippines.

REFERENCES

Abrahamson, N.J. 1971. Computer programs for fish stock assessment. FAO Fish.Tech.Rep. (101):pag. var.

Bakun, A. and R.H. Parrish. 1981. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In Workshop on the effect of environmental variation on the survival of larval pelagic fishes (G.D. Sharp, ed.). IOC Workshop Report No.28. UNESCO, Paris. 323 p.

Bakun, A., J. Bayer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean science in relation to living resources. Can.J.Fish.Aquat.Sci. 39(7):1059-1070.

Dickerson, R.E. 1928. Distribution of life in the Philippines. Bur.Sci.Monogr. (Philippines) No.21. 222 p. + plates.

Ingles, J. and D. Pauly. 1982. Raw data and intermediate results for an atlas of the growth, mortality and recruitment of Philippine fishes. i-xv + 224 p. (mimeo).

___________. (In press). An atlas of the growth, mortality and recruitment of Philippine fishes. ICLARM Tech.Rep.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env.Biol.Fish 3:65-84.

Munro, J.L. (In press). Some advances and developments in coral reef fisheries research. Proc.Gulf Caribb.Fish.Inst. 35.

Pauly, D. 1982. Studying single species in a multispecies context. pp. 33-70. In Theory and management of tropical fisheries (D. Pauly and G.I. Murphy, eds). ICLARM Conference Proceedings 9, Manila, Philippines. 360 p.

Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28(4):205-211.

Pauly, D. and J. Ingles. 1981. Aspects of the growth and mortality of exploited coral reef fishes. pp. 81-98. In Proceedings of the Fourth International Coral Reef Symposium, Manila, Philippines (E. Gomez, C.E. Birkeland, R.W. Buddemeyer, R.E. Johannes, J.A. Marsh, Jr. and R.T. Tsuda, eds). Vol.1.

Pauly, D., N. David and J. Ingles. 1982. ELEFAN II: User's instruction and program listings. Mimeo, pag. var.

Tan, E.O. 1970. Notes on the biology of chub mackerel Rastrelliger brachysoma (Bleeker), in Manila Bay. pp. 479-480. In The Kuroshio, A Symposium of the Japan Current (J.C. Marr, ed.). East-West Center Press, Honolulu. 614 p.

Tiews, K. and P. Caces-Borja. 1965. On the availability of fish of the family Leiognathidae Lacépède in Manila Bay and San Miguel Bay on their accessibility to controversial fishing gears. Philipp.J.Fish. 7:59-86.

Tiews, K., A.N. Mines and I.A. Ronquillo. 1972. On the biology of Saurida tumbil (Block 1801) Family Synodontidae in Philippine waters. Proc.Indo-Pac.Fish.Counc. 13(3):100-120.

Tiews, K., I.A. Ronquillo and P. Caces-Borja. 1975a. On the biology of roundscads (Decapterus Bleeker) in Philippine waters. Philipp.J.Fish. 9:45-71.

Tiews, K., I.A. Ronquillo and L.M. Santos. 1975b. On the biology of anchovies (Stolephorus Lacépède) in Philippine waters. Philipp.J.Fish. 9:92-123.

Weber, W. 1976. The influence of hydrographical factors on the spawning time of tropical fish. pp. 269-281. In Fisheries resources and their management in Southeast Asia (K. Tiews, ed.). West Berlin. 522 p.

LOS DESOVES Y DISTRIBUCION LARVAL DE CUATRO ESPECIES PELAGICAS Y SUS RELACIONES CON LAS VARIACIONES DEL AMBIENTE MARINO FRENTE AL PERU

por

Haydee Santander
y
Roberto Flores

Instituto del Mar del Perū
Apartado 22
Callao - PERU

Summary

The temporal-spatial variations and interactions with spawning and larval distribution of the anchoveta (*Engraulis ringens*); sardine (*Sardinops sagax sagax*); jack mackerel (*Trachurus murphyi*); and mackerel (*Scomber japonicus peruanus*) are analysed in relation with environmental conditions as expressed by thermal and salinity structure, coastal upwelling and superficial currents from 1964-1982.

Representative data from this period are included, particularly on the principal spawning and larval abundance areas for these species, for selected areas which emphasize the El Niño periods of 1965, 1972-73, and 1976-77; and also the anti-El Niño periods of 1964, 1967, and 1970-71.

INTRODUCCION

Las especies de peces pelágicos, particularmente los Cupleidae, sufren grandes fluctuaciones en la abundancia de sus poblaciones, motivadas por la alta variabilidad del reclutamiento. Entre las causas atribuibles estan la intensidad del desove y sobrevivencia de sus huevos y larvas, las que a su vez parecen ser influenciadas por la oportunidad en la ocurrencia del desove en espacio y tiempo. Es indudable que el alimento es fundamental para la sobrevivencia de las larvas, asi como las condiciones ambientales que determinan la secuencia de los diferentes tipos de alimento apropiado para cada etapa de vida hasta recluta.

Los resultados de Ware et al.(1980) sugieren que las larvas de anchoveta *Engraulis ringens* requieren de fitoplancton solamente en la primera semana de vida, mientras que en la transición a la fase de crecimiento necesitan de mayor habilidad para hallar su ración adecuada de zooplancton. Lo que significa que la época y área del desove de estos peces juega un papel fundamental en la sobrevivencia de estas fases. Por lo tanto, de todo el rango de la distribución de las especies, las áreas de desove seleccionadas a través del tiempo, deben proveer las condiciones más apropiadas para la crianza.

En esta contribución se presentan resultados del análisis de los desoves y/o distribución larval de las cuatro principales especies pelágicas frente al Perú: anchoveta (*Engraulis ringens*) sardina (*Sardinops sagax*), jurel (*Trachurus symmetricus murphyi*) y caballa (*Scomber japonicus peruanus*). Se discute también su relación con algunos procesos ambientales, en particular bajo condiciones denominadas normales y los que presentan anomalías conocidos como años "El Niño".

CARACTERISTICAS DE LOS DESOVES Y DISTRIBUCION DE LARVAS

Anchoveta

El desove de la anchoveta se extiende en casi toda la costa del Perú, desde Cabo Blanco (03°30'S) hasta 18°30'S y en Chile hasta la latitud de 25°40'S. Sin embargo, el área más importante por la intensidad y frecuencia de los desoves es la comprendida entre 06°00' y 14°00'S.

Esta área reune condiciones muy peculiares, siendo la más importante la configuración de la plataforma, cuya mayor amplitud se presenta entre 7° y 10°S.

La línea costera entre 6° y 14°S tiene una orientación SSE (150°), que resulta casi paralela a la dirección predominante de los vientos alisios del SE. En esta área no se presentan las zonas de gran divergencia tan notables que existen entre Talara y Pta. Falsa (04°30' - 06°00'S) y entre Pisco y San Juan (14° -15°S). Los remolinos frecuentes se registran principalmente al norte de 7°, entre 6° y 7°S y al sur de 12°, entre 12° y 14°S.

Los vientos en toda la costa son más fuertes en Invierno y más débiles en Verano. Particularmente frente a Chimbote (9°S) son más estables, siendo en promedio de 4.6 m/seg. Las áreas de afloramiento que varían ligeramente de posición cada año y se ubican principalmente entre 7°, 8°, 9°, 10°, 11° y 12°S, donde los procesos son sostenidos y no de gran intensidad.

En el período de enfriamiento, el afloramiento se intensifica y se desplaza hacia el norte, ampliándose latitudinalmente.

Según Guillén y Calienes (1981), las aguas afloradas de Chimbote provienen de una extensión de la Corriente de Cronwell durante la mayor parte del año, principalmente en Otoño e Invierno, y están caracterizadas por un mayor contenido de oxígeno. El ancho promedio de la zona de afloramiento es de 60 km., similar al de Paita (05°00'S) y San Juan (15°S) (Zuta et al., 1978) y su profundidad es mayor que frente a Callao y San Juan en invierno (Tabla Nº 1).

TABLA N°1 VARIACION ESTACIONAL EN LAS AREAS DE AFLORAMIENTO FRENTE AL PERU (de Guillén y Calienses, 1981)

Area	Isopycnas (σ_t)	Profundidad de afloramiento (m)	Vientos Promedio (m/s)	Mes	Velocidad (cm/s)	Período de enfriamiento
Paita:(1)						
Otoño	25.3-25.5	50	4.9(7)	Mayo	$4.6x10^{-4}$	Abril-Agosto (5 meses)
Invierno	25.8-26.1	150		Septiembre	$2.2x10^{-3}$	
		Promedio 100			Prom $1.3x10^{-3}$	
Chimbote:						
Otoño	25.4-25.6	50	4.6	Mayo	$3.9x10^{-4}$	Marzo-Octubre (8 meses)
Invierno	25.8-26.0	120		Septiembre	$1.5x10^{-3}$	
		Promedio 85			Prom $0.9x10^{-3}$	
Callao:(2)						
Otoño	25.5-25.8	40	3.2(7)	Mayo	$6\ x10^{-4}$	Abril-Septiembre (6 meses)
Invierno	25.6-25.9	60		Septiembre	$3.8x10^{-3}$	
		Promedio 50			Prom $2.2x10^{-3}$	
San Juan:(1)						
Otoño	25.6-25.8	40	4.8(7)	Junio	$2.1x10^{-3}$	Abril-Septiembre (6 meses)
Invierno	25.8-26.1	70		Agosto	$4.0x10^{-3}$	
		Promedio 55			Prom $3.1x10^{-3}$	
Oregon:(3)					$2-0.5x10^{-2}$	
Oregon:(4)					$0.2-7.0x10^{-3}$	
Noroeste Africa:(5)					10^{-1}	
Baja California:(6)					$5.4-7.9x10^{-3}$	

(1) Zuta et al. (1978); (2) Flores (unpublished data) (3) Halpern (1976); (4) Smith, Pattullo, and Lane (1966); (5) Barton, Huyer and Smith (1977); (6) Stevenson (1974); (7) Zuta and Guillén (1970).

En Chimbote, el período de enfriamiento dura 8 meses (Marzo-Octubre), siendo mayor que para otras áreas.

Tanto Walsh *et al*. (1980), Brockman *et al*. (1980) y Shaffer (1982) coinciden al afirmar que hay una mayor estabilidad del ambiente físico en el área norte, comparada con el sur (15°S) en términos de vientos, corrientes y variabilidad termal.

El desove se distribuye principalmente en áreas costeras que corresponden a las Aguas costeras Frías, de salinidades entre 34.9 y 35.0°/oo (Fig. 1a). La extensión de las áreas de distribución de huevos y crianza de larvas ha variado mucho desde la década del 60, no solamente por efecto de la reducción de la población que se producía en los últimos años de esta década, sino también por acción de las anomalías del ambiente, principalmente desde el Fenómeno "El Niño" 1972-73. Si bien, el efecto de las anomalías ambientales, expresadas en la invasión de las Aguas Ecuatoriales Superficiales (AES) y/o en el avance de las Aguas Subtropicales Superficiales (ASTS) son temporales; cuando ocurren a bajos niveles poblacionales, las consecuencias son más drásticas y más prolongadas.

La máxima extensión del desove fue observada en 1966-1967, hasta más allá de 120 millas de la costa, con altas concentraciones mayores a 2000 huevos por metro cuadrado (Fig. 2b). Sin embargo, estas áreas de distribución son en parte el producto de la dinámica del agua. En Agosto de 1967, donde se registró la mayor amplitud del desove, la topografía de 15°C (Fig. 2a) mostró flujos superficiales predominantemente hacia el norte con la presencia de remolinos ciclónicos que influirían en la concentración de los organismos, como fue detectado a través de la distribución del desove.

Las áreas donde se producen los desoves se ubican actualmente entre 5 y 20 millas de la costa. En Agosto-Septiembre de 1981 se localizaron 18 focos mayores en el momento del desove (Estadío I, recientemente desovados), entre 07°00'S y 13°00'S. El 28% de estos focos de desove se presentaron a 8 millas de la costa, 22% a 17 millas, 17% a 5 millas y otro 14% a 14 millas.

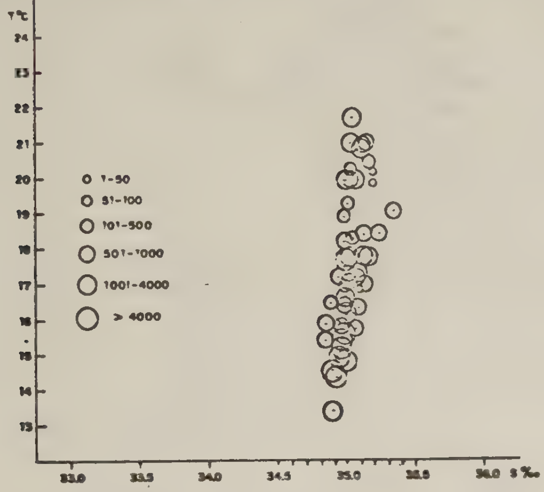


Fig. 1a. Distribución T/S de Huevos de Anchoveta.

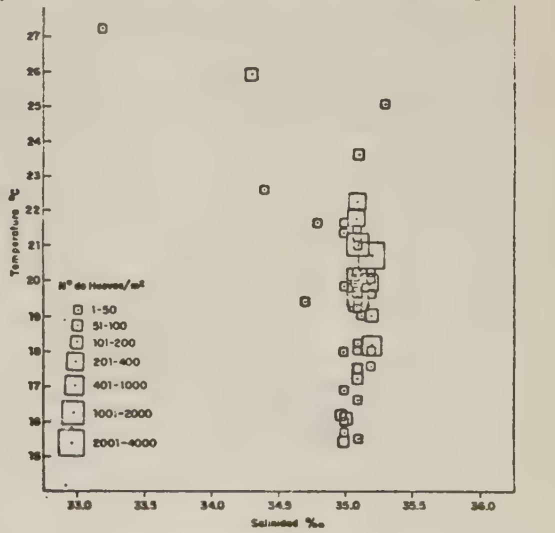


Fig.1b.- Distribución en diagrama T/S de huevos de Sardina.

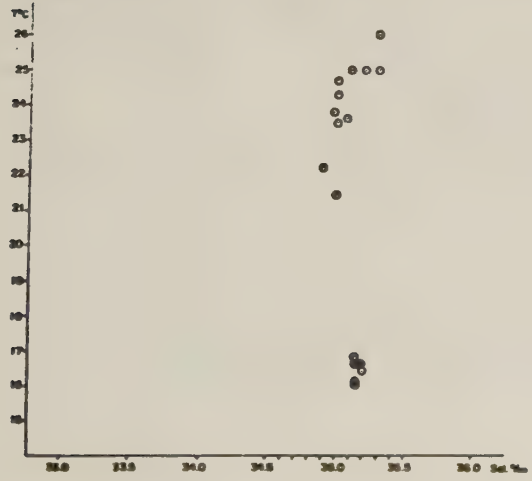


Fig.1c. Distribución T/S de Larvas de Jurel

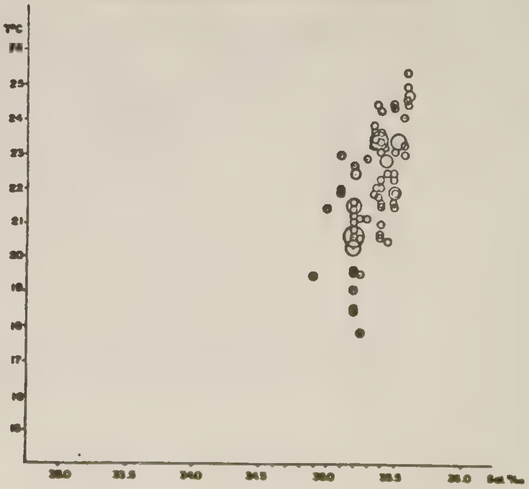


Fig.1d. Distribución T/S de Larvas de Caballa

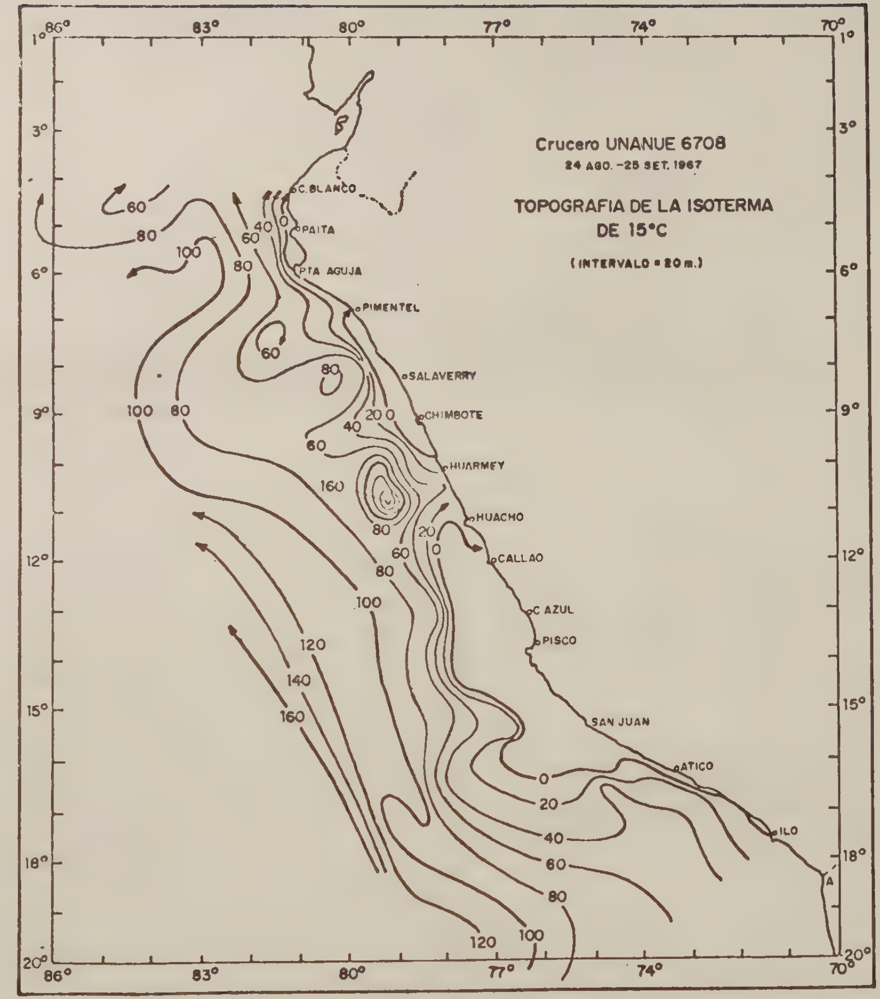

Crucero UNANUE 6708
24 AGO. -25 SET. 1967
TOPOGRAFIA DE LA ISOTERMA DE 15°C
(INTERVALO = 20 m.)
86°
83°
80°
77°
74°
70°
1°
3°
6°
9°
12°
15°
18°
20°
C. BLANCO
PAITA
PTA AGUJA
PIMENTEL
SALAVERRY
CHIMBOTE
HUARMEY
HUACHO
CALLAO
C AZUL
PISCO
SAN JUAN
ATICO
ILO
A
0
10
20
40
60
80
100
120
140
160

Fig. 2a.

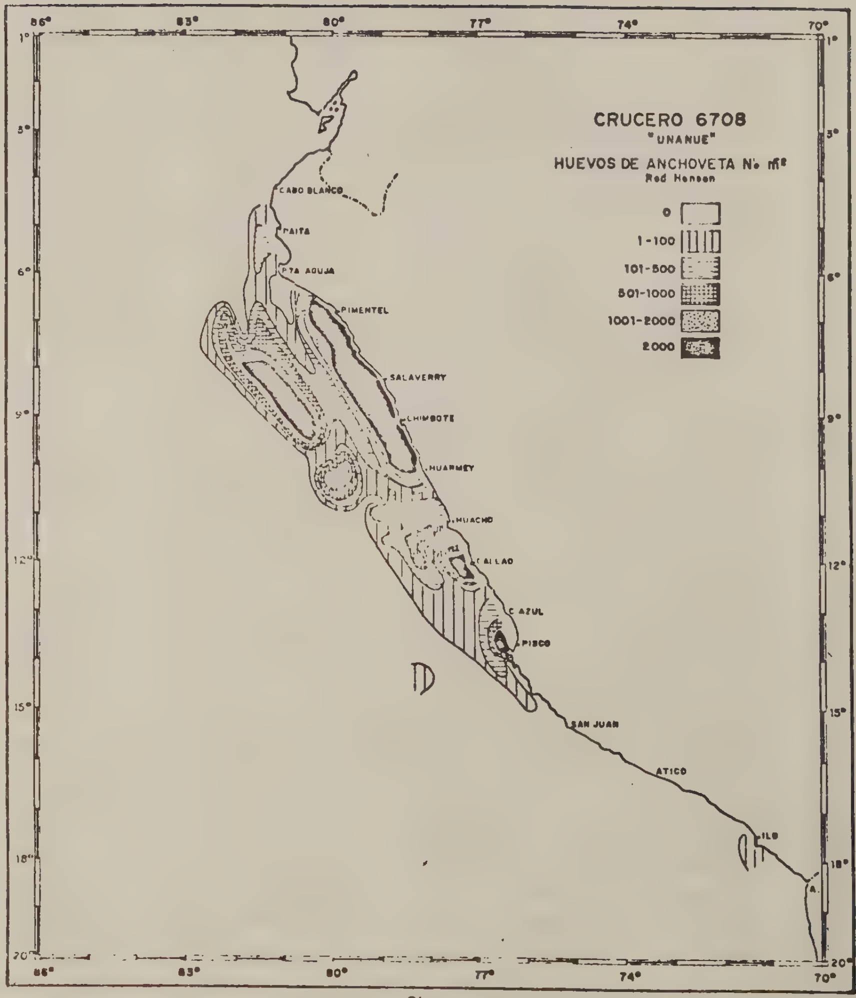

CRUCERO 6708
"UNANUE"
HUEVOS DE ANCHOVETA Nº m²
Red Hensen
0
1-100
101-500
501-1000
1001-2000
2000
86°
83°
80°
77°
74°
70°
1°
3°
6°
9°
12°
15°
18°
20°
CABO BLANCO
PAITA
PTA AGUJA
PIMENTEL
SALAVERRY
CHIMBOTE
HUARMEY
HUACHO
CALLAO
C AZUL
PISCO
SAN JUAN
ATICO
ILO
A

Fig. 2b.

Fig. 2a.- Distribución de huevos de anchoveta.

Fig. 2b.- Topografía de la isoterma de 15ºC en el Crucero 6708. 24 de Agosto - 25 de Septiembre, 1967.

Como rasgo común, todos los focos de desove estuvieron ubicados por fuera de los focos de afloramiento. Una de las características observadas a través del tiempo es que las áreas de máximo desove no co-ocurren con los focos de máximo afloramiento y en el sur donde se encuentra el área más intensa de afloramiento, los desoves son menores (SANTANDER, 1981 b) (Fig. 3). Sin embargo, después de 1972 se han registrado desoves con mayor frecuencia al sur de 14ºS.

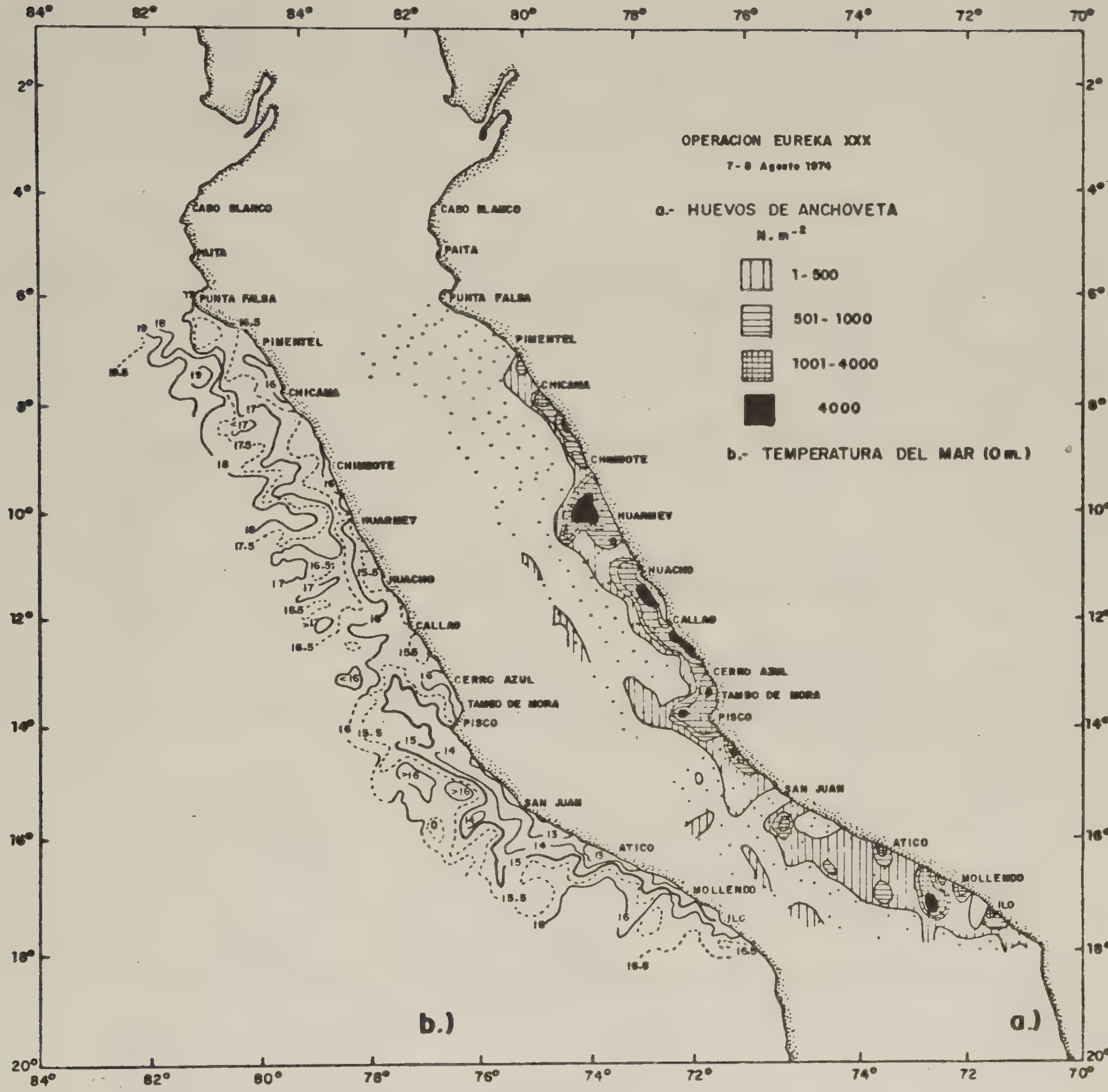

OPERACION EUREKA XXX
7-8 Agosto 1974
a.- HUEVOS DE ANCHOVETA
N.m-2
1-500
501-1000
1001-4000
4000
b.- TEMPERATURA DEL MAR (0 m.)
CABO BLANCO
PAITA
PUNTA FALSA
PIMENTEL
CHICAMA
CHIMBOTE
HUARMEY
HUACHO
CALLAO
CERRO AZUL
TAMBO DE MORA
PISCO
SAN JUAN
ATICO
MOLLENDO
ILO
b.)
a.)
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 3

Fig. 3.- Temperatura superficial (ºC) en la Operación EUREKA XXX. 7/8 Agosto, 1974.

En la Fig. 4 se han graficado los índices de desove (promedio de huevos por estación) para cada 2 grados latitudinales en la época de máximo desove. Se aprecia que en los años de 1965 a 1971, los desoves al sur de 14°S eran muy esporádicos y mayormente limitados al área de 14° a 16°S. En 1972 se experimentaron los efectos del Fenómeno "El Niño" desde Febrero y el patrón de distribución latitudinal cambió por el desplazamiento de los cardúmenes de anchoveta hacia el sur. Consecuentemente ese año los desoves se produjeron principalmente entre 10° y 14°S y al sur de 16°S. En los años siguientes se siguen presentando estos desoves al sur de 14°S, hasta 18°30'S.

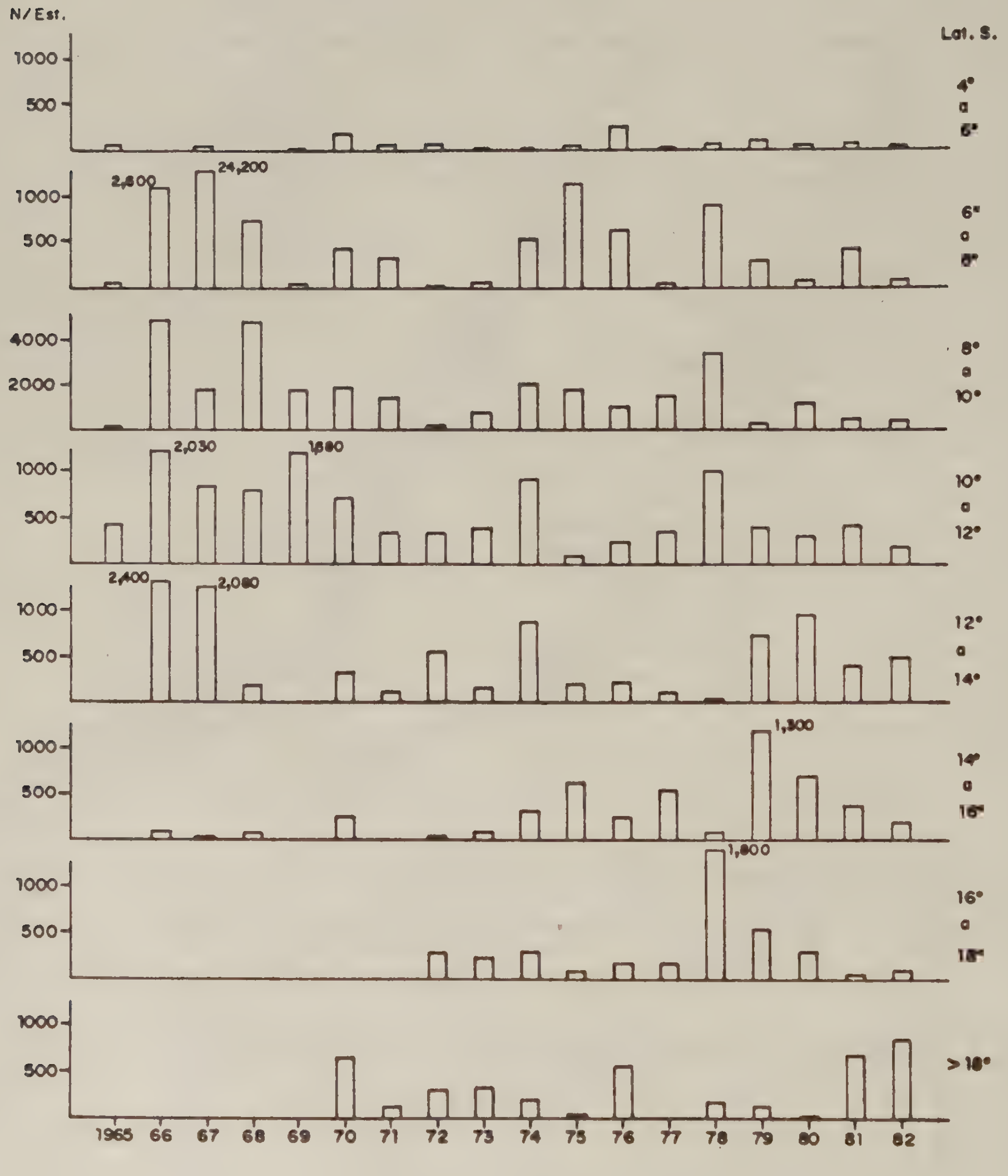


Fig. 4.- Distribución latitudinal del desove de anchoveta en invierno, de 1965 a 1982.

Dos posibles factores parecen haber influido en esta selección de nuevas áreas de desove; inicialmente como un efecto de las condiciones ambientales de 1972-73 y posteriormente por la alteración de las condiciones ambientales expresadas principalmente por un más frecuente avance de ASTS hacia la costa, en el período de desove. Una consecuencia de esta mayor penetración de las ASTS es la ocurrencia de desoves de sardina en áreas cada vez más próximas a la costa, lo que contribuye a que la sardina se constituya en competidor y predador de la anchoveta cuando co-ocurren las áreas de desove y de distribución larval.

Hasta 1971 se desarrollaba un ciclo de desove típico de Julio a Marzo, con un pico en Septiembre al final de la estación de Invierno. Este patrón estacional tiene una relativa relación con el ciclo de afloramiento: no coinciden sus máximos. En Invierno ocurre el máximo afloramiento, y al final de Invierno el máximo del desove. Sin embargo, si se observa correspondencia entre la secuencia de la producción fitoplanctónica y el zooplancton (Santander, 1974; Mendiola y Ochoa 1980) con el máximo del desove como consecuencia del ciclo de afloramiento.

Sardina

El área de desove de sardina ha experimentado grandes variaciones, tanto en extensión latitudinal como de distancia de la costa, pudiendo diferenciarse que a partir de 1972 se ha registrado una mayor expansión en ambos sentidos (Santander 1981 a).

De 1966 a 1971, los desoves fueron muy pobres y limitados al área norte principalmente (Fig. 5), con las mayores concentraciones en los períodos más cálidos, como en 1969.

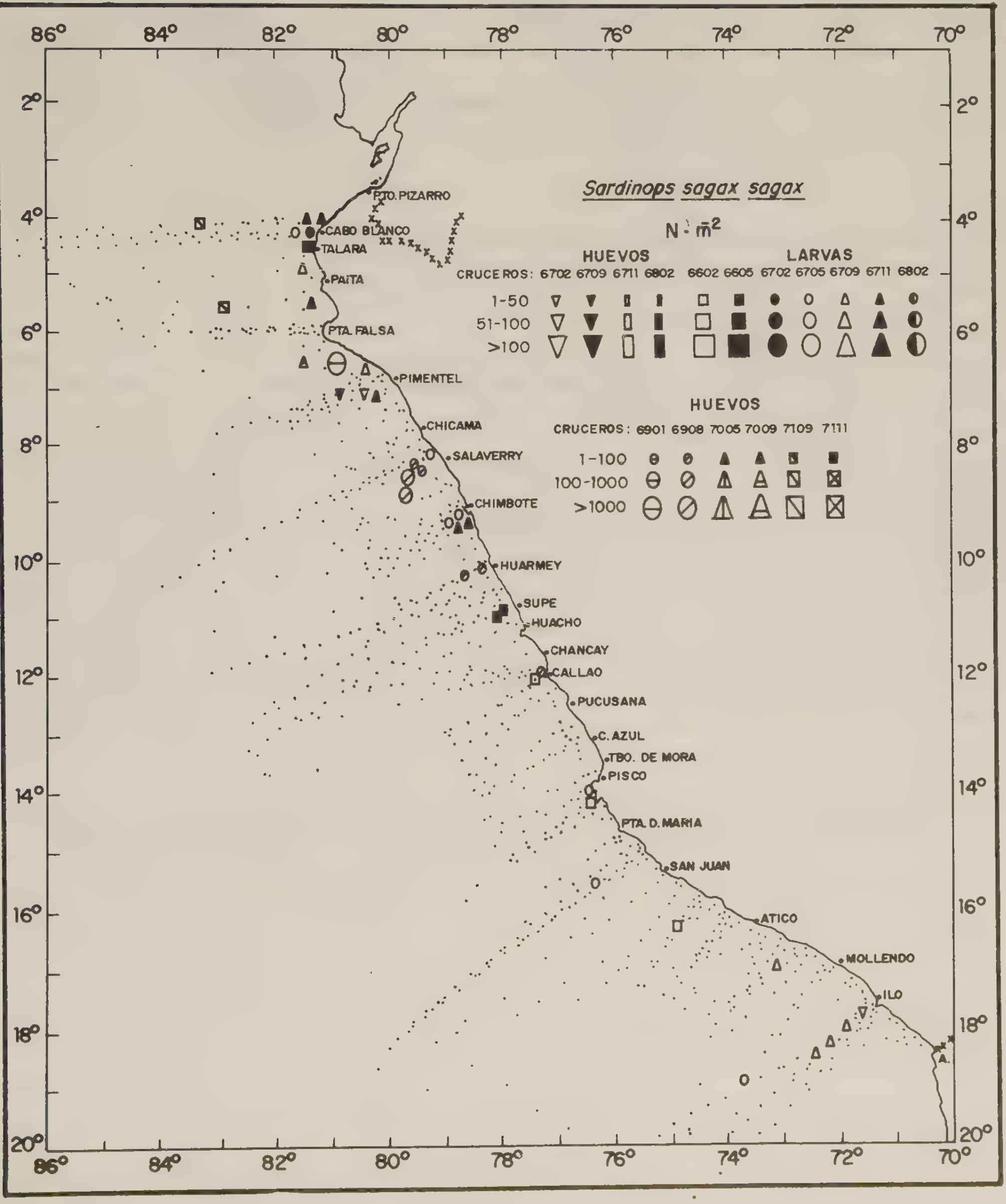

86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°
Sardinops sagax sagax
N · m̄2
HUEVOS
LARVAS
CRUCEROS: 6702 6709 6711 6802 6602 6605 6702 6705 6709 6711 6802
1-50
51-100
>100
HUEVOS
CRUCEROS: 6901 6908 7005 7009 7109 7111
1-100
100-1000
>1000
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
C. AZUL
TBO. DE MORA
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
A.
Fig. 5

Fig. 5.- Distribución de huevos y larvas de sardina, de 1966 a 1971.

Actualmente, el área de distribución se extiende prácticamente a toda el área frente a la costa, de 03°30' a 18°30'S (Fig. 6). Pero las más frecuentes y mayores concentraciones del desove se dan entre 5° y 12°S. Estas áreas se encuentran cada vez más próximas a la costa, con las mayores concentraciones a 10 ó 20 millas de distancia a la costa, colindante con la anchoveta (Fig. 7). El mayor o menor acercamiento hacia la costa está relacionado con la extensión de las ASTS, con salinidad superior a 35.0°/oo (Fig. 15).

El ciclo de desove incluye 9 meses, de Julio a Marzo y el máximo usualmente se produce a fines de Invierno.

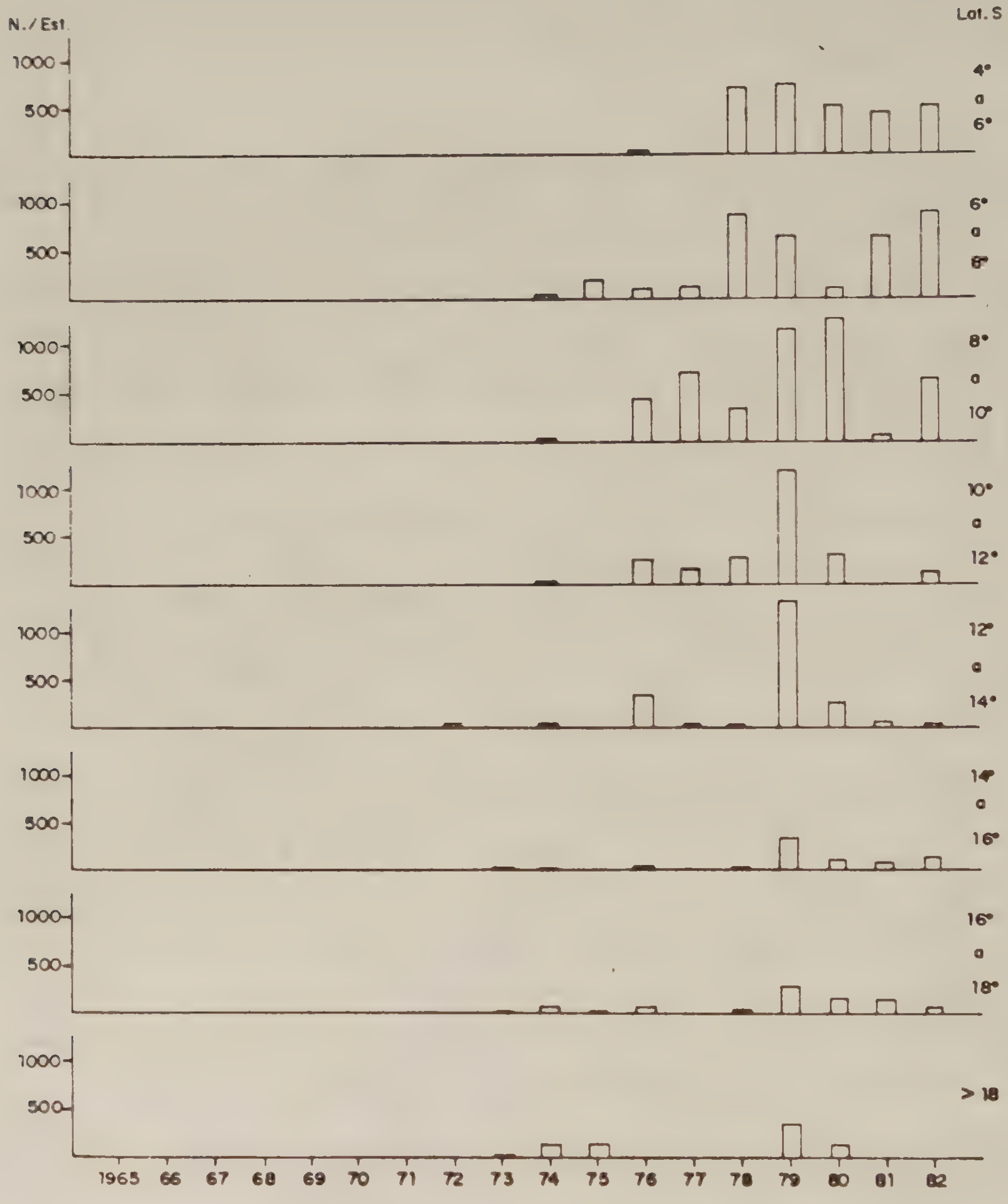


Fig. 6.- Distribución latitudinal del desove de sardina en invierno, de 1965 a 1982.

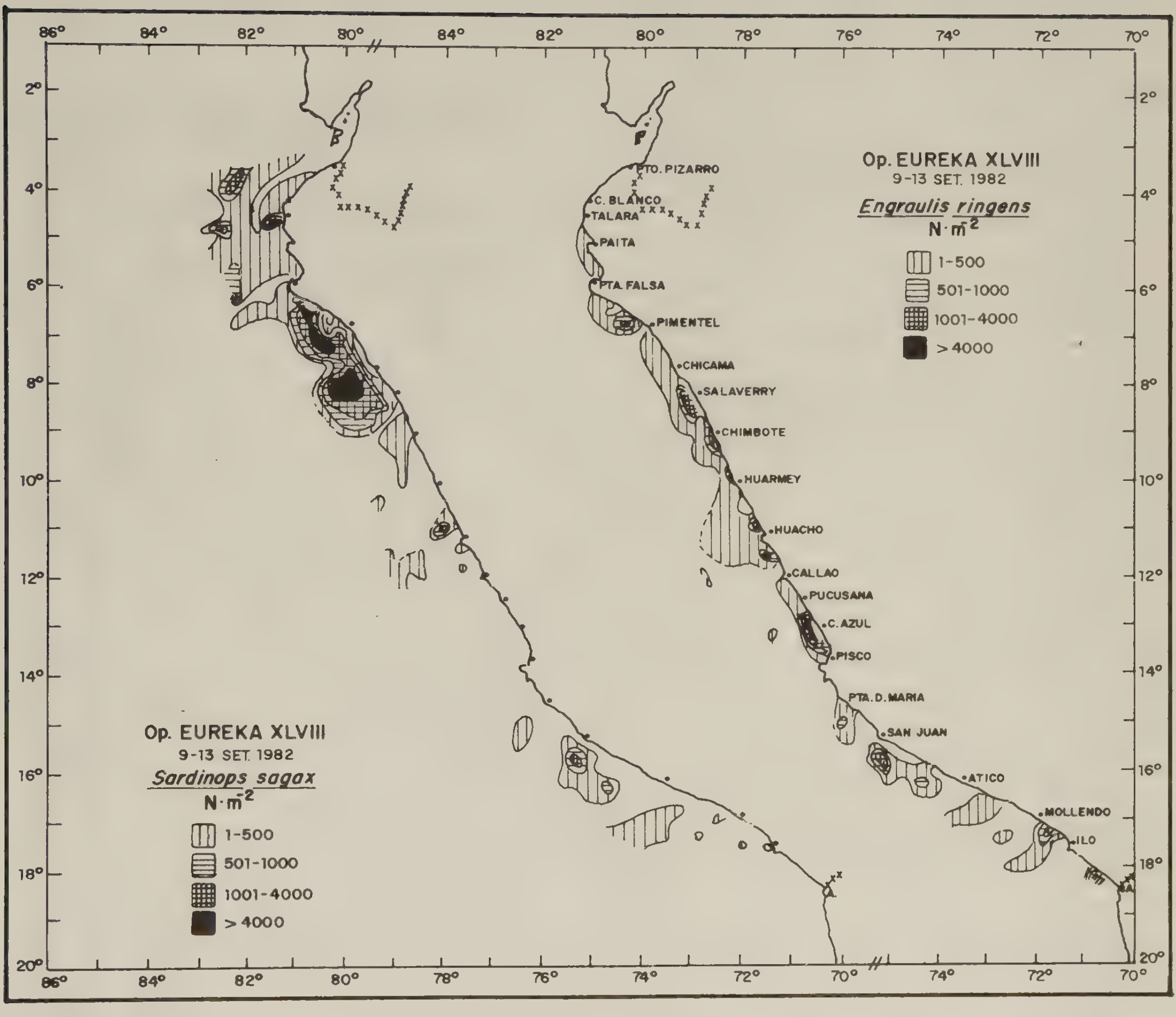

Op. EUREKA XLVIII
9-13 SET. 1982
Sardinops sagax
N·m^{-2}
1-500
501-1000
1001-4000
> 4000
Op. EUREKA XLVIII
9-13 SET. 1982
Engraulis ringens
N·m^{-2}
1-500
501-1000
1001-4000
> 4000
PTO. PIZARRO
C. BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
HUACHO
CALLAO
PUCUSANA
C. AZUL
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 7

Fig. 7.- Distribución del desove de sardina en la Operación EUREKA XLVIII. 9/13 Septiembre, 1982.

Jurel

La distribución del desove de jurel se ubica principalmente en el área sur, de 16°00' a 18°30'S, aunque se han registrado desoves en diferentes puntos del litoral desde 13°00' hacia el norte, en muy bajas concentraciones. Esta área se extiende a más de 120 millas de la costa.

El área principal de distribución larval, abarca una extención de alrededor de 300 millas de la costa de Mollendo (17°00'S) pero las mayores concentraciones se ubican dentro de 60 millas de la costa (Fig. 8).

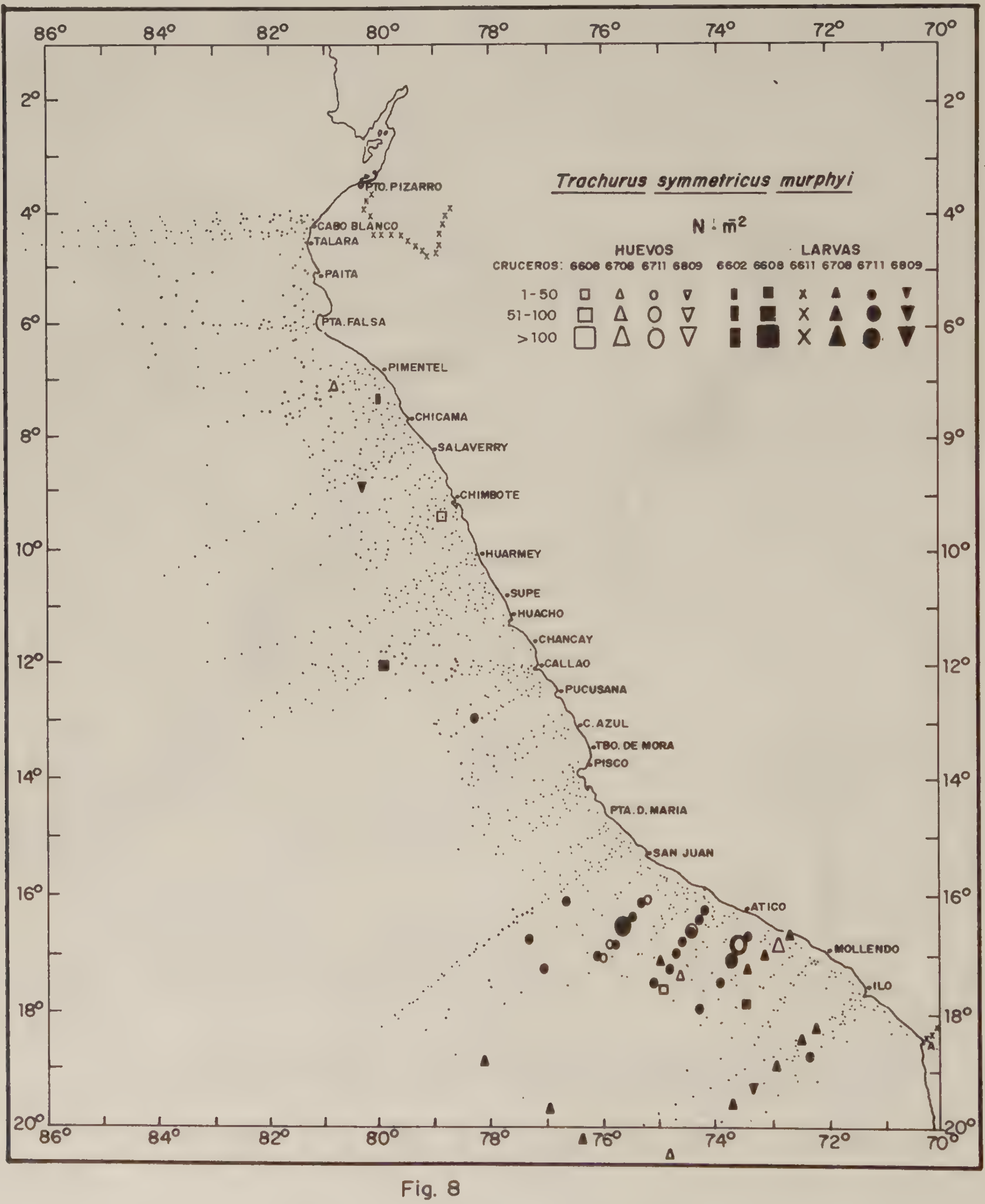

Trachurus symmetricus murphyi
N · m̄²
HUEVOS
LARVAS
CRUCEROS: 6608 6708 6711 6809 6602 6608 6611 6708 6711 6809
1-50
51-100
>100
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
9°
10°
12°
14°
16°
18°
20°
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
C. AZUL
TBO. DE MORA
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO

Fig. 8

Fig. 8.- Distribución de huevos y larvas de jurel, de 1966 a 1968.

Esta área de distribución está asociada a los bordes de los afloramientos intensos del sur (14° - 16°S), cuyas fuentes principales son las aguas de la sub-antártida (aguas frías y de baja salinidad, ricas en nutrientes), y del frente de estas aguas con las ASTS, con temperaturas mayores a 16°C y salinidades mayores a 35.0°/oo en la superficie (Fig. 1c) que dominan las áreas por fuera de las 60 millas de la costa, aproximándose principalmente en Abril y replegándose por fuera de 90 millas de la costa, en Julio, Agosto, y Septiembre principalmente (Fig. 9). En estos meses, estas áreas son ocupadas por aguas de la corriente costera y las afloradas que se presentan mayormente en Septiembre. En el área al sur de 14°S, a diferencia del área norte-central, la plataforma continental es muy angosta; la línea costera tiene una orientación SE (130°), que resulta totalmente pararela a los vientos alisios del SE. Entre Pisco y San Juan (14° - 15°20'S) se presentan zonas de gran divergencia y en Pisco (14°S) son frecuentes los remolinos. Los vientos son de mayor intensidad y persistencia que en las otras áreas de afloramiento, siendo más débiles en marzo y mayo (fines de Verano y Otoño) y más intensos de Junio a Septiembre (Invierno), fluctuando entre 1.3 m/seg (Marzo) y 8.8 m/seg (Junio) con un promedio de 4.8 m/seg (Zuta y Guillén, 1970).

El desove de jurel se produce de Invieno a Verano (Julio Marzo), con una mayor intensidad a fines de Invierno en Septiembre.

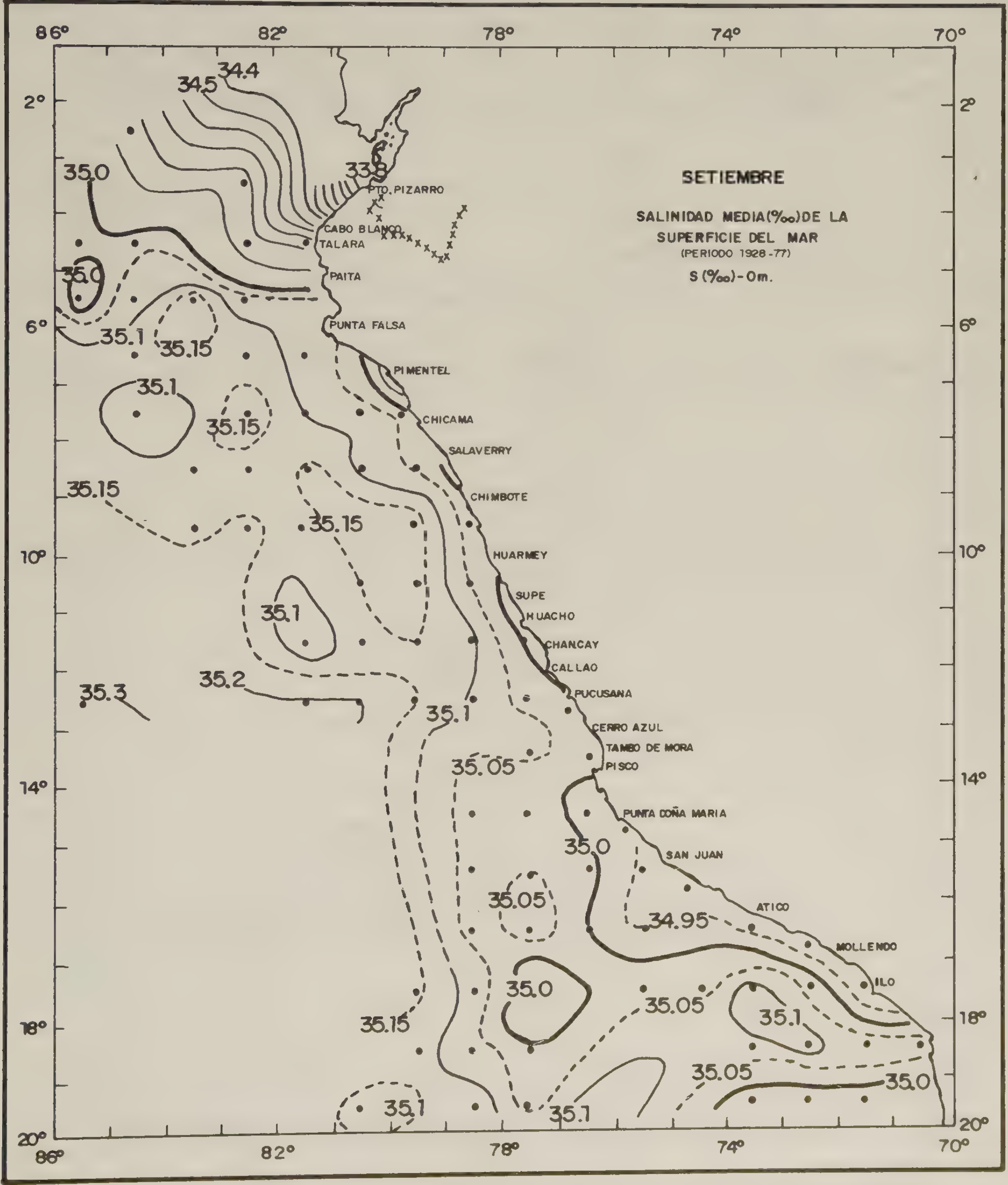

86°
82°
78°
74°
70°
2°
6°
10°
14°
18°
20°
SETIEMBRE
SALINIDAD MEDIA(‰)DE LA SUPERFICIE DEL MAR
(PERIODO 1928-77)
S (‰)-Om.
34.4
34.5
35.0
33.8
35.1
35.15
35.2
35.3
35.05
34.95
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PUNTA FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
CERRO AZUL
TAMBO DE MORA
PISCO
PUNTA DOÑA MARIA
SAN JUAN
ATICO
MOLLENDO
ILO

Fig. 9.- Salinidad promedio (o/oo) de la superficie del mar en Septiembre. Período 1928-1977. (de Urquizo y Morón, No publicado).

Caballa

El desove de caballa se distribuye en casi toda la costa, de 03°30' a 18°30'S, desde muy cerca de la costa hasta más allá de las 140 millas.

Esta especie desova de Agosto a Marzo, siendo principalmente desovadora de Verano.

En los años 1966 a 1968, el desove se producía en el área norte-central principalmente, de 03°30' a 15°00'S (Fig. 10), y en el período de "El Niño" 1972-73, uno de los grupos del ictioplancton de mayor frecuencia y densidad a lo largo de toda la costa fue el de los Scombridae, siendo la "caballa" uno de sus principales componentes.

La distribución de las larvas de esta especie, coincide con la de las aguas subtropicales superficiales (Fig. 1d), y experimentan incrementos considerables en su distribución y densidad con el avance de estas aguas.

Las mayores concentraciones por fuera de las 60 millas de la costa, están relacionadas con el predominio de estas aguas que están presentes durante todo el año y que avanzan hacia la costa de Mayo a Julio, principalmente al norte de 14°S; mientras que reduce su avance de Julio a Septiembre, en especial en el área sur, por fuera de 90 millas.

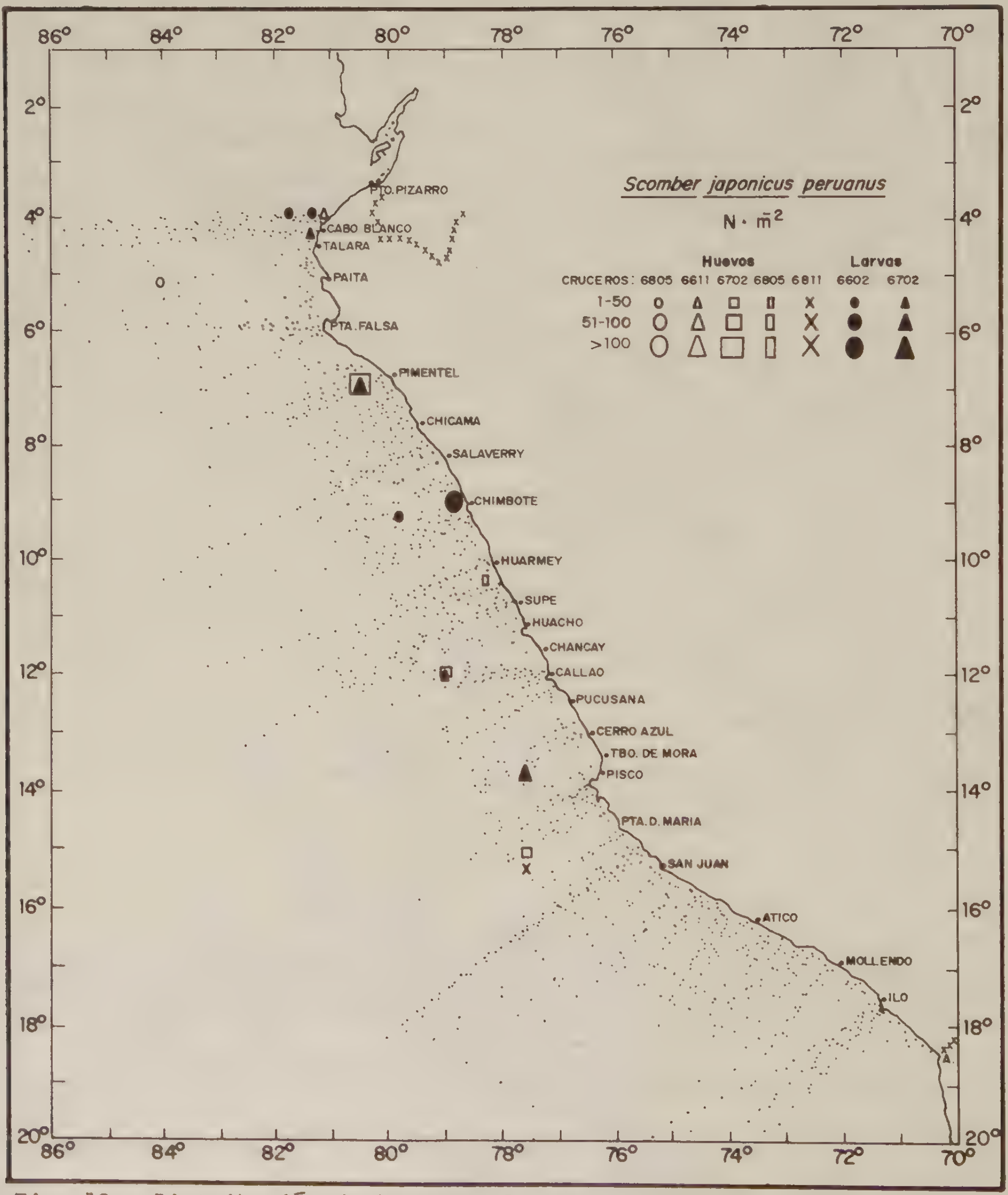

86° 84° 82° 80° 78° 76° 74° 72° 70°
2° 4° 6° 8° 10° 12° 14° 16° 18° 20°
Scomber japonicus peruanus
N · m̄2
Huevos
Larvas
CRUCEROS: 6805 6611 6702 6805 6811 6602 6702
1-50 ○ △ □ ▯ X ● ▲
51-100 ○ △ □ ▯ X ● ▲
>100 ○ △ □ ▯ X ● ▲
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
CERRO AZUL
TBO. DE MORA
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO

Fig. 10.- Distribución de huevos y larvas de caballa, de 1966 a 1968.

FLUCTUACIONES RELACIONADAS CON EL AMBIENTE

Sin la acción de las pesquerías, la anchoveta durante milenios ha dominado el ecosistema costero frente al Perú (De Vries y Pearcy, 1980), a diferencia de otros sistemas como el de California, donde se produjeron grandes cambios en abundancia de los recursos pelágicos en los dos últimos siglos.

La información de desove y de distribución larval de anchoveta desde 1961, muestra que los períodos de condiciones ambientales ligeramente fríos como 1966, 1967, 1975 le son favorables; en estos períodos ocupan ampliamente el área de desove y el máximo se produce a fines de Invierno.

Durante los fenómenos "El Niño" de 1965, 1972 y 1976, de diferente magnitud y forma de manifestarse, los efectos en los recursos también fueron diferentes.

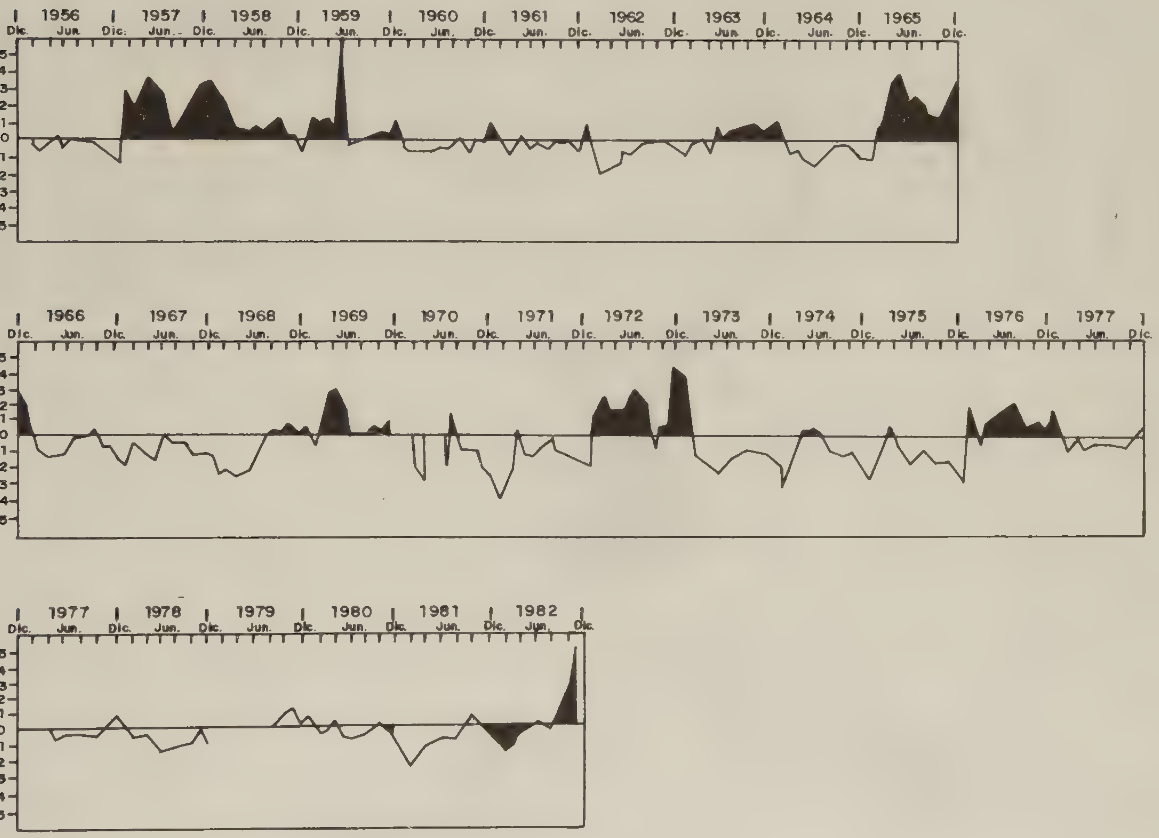


Fig. 11

Fig. 11.- Variación anual de temperatura superficial en Chicama (07°43'LS) (datos hasta Abril de 1977 de Guillén y Calienes, 1980).

Durante 1965, la mayor intensidad del Fenómeno ocurrió durante Marzo y Abril, y fue originado por Aguas Ecuatoriales Superficiales (Temperatura Sup. 24° - 27°C, y Salinidad de 33.0 - 34.8°/oo).

Durante el Invierno de este año dominaron las Aguas Subtropicales superficiales en toda la costa, y las aguas frías ocuparon solamente las áreas muy próximas a la costa.

Las áreas de desove se mantuvieron en las áreas norte-central, (Fig. 12) pero el desove fue pobre, aun cuando el nivel de la población era alto, alrededor de 16 millones de toneladas. El ciclo de desove mostró que en Primavera este fue ligeramente mayor que en Invierno cuando las Aguas Costeras Frías ocuparon una mayor extensión.

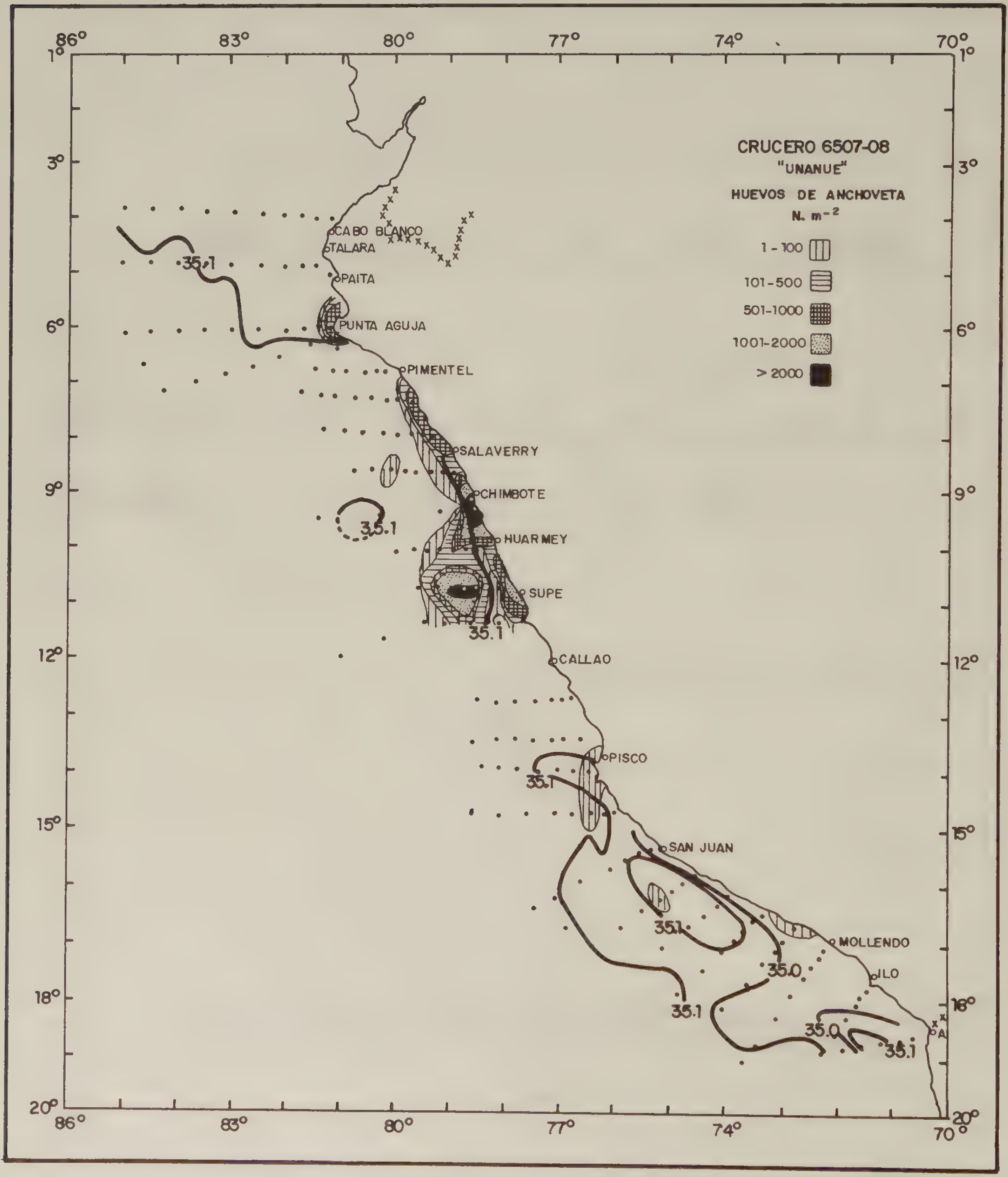

86°
83°
80°
77°
74°
70°
1°
3°
6°
9°
12°
15°
18°
20°
CRUCERO 6507-08
"UNANUE"
HUEVOS DE ANCHOVETA
N. m⁻²
1 - 100
101-500
501-1000
1001-2000
> 2000
CABO BLANCO
TALARA
PAITA
PUNTA AGUJA
PIMENTEL
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
CALLAO
PISCO
SAN JUAN
MOLLENDO
ILO
A
35.1
35.0

Fig. 12

Fig. 12.- Distribución de huevos de anchoveta en el Crucero 6507-08. 8 Julio - 10 Septiembre, 1965.

"El Niño" 1972-73, de gran magnitud especialmente por su larga duración (Febrero 1972-Febrero 1973) y sus efectos más intensos, se manifestaron durante el avance de las AES en dos fases: la primera de Febrero a Junio de 1972 y la segunda de Diciembre 1972 a Febrero 1973. En el segundo semestre de 1972 después de la fase inicial del fenómeno, cuando las aguas ecuatoriales se retrajeron hasta el norte de Talara (04°30'S), las Aguas Subtropicales Superficiales, con salinidades mayores a 35.1 °/oo jugaron un rol dominante, particularmente entre Agosto y Noviembre, de tal forma que el área entre Talara y Callao fue casi homosalina (Zuta et al., 1976). En estas circunstancias, aun cuando las AES estaban replegadas hacia el norte, el desove se desplazó hacia el centro y sur, limitado a 20 millas de la costa por acción de las Aguas Subtropicales Superficiales y fue muy reducido (Fig.13).

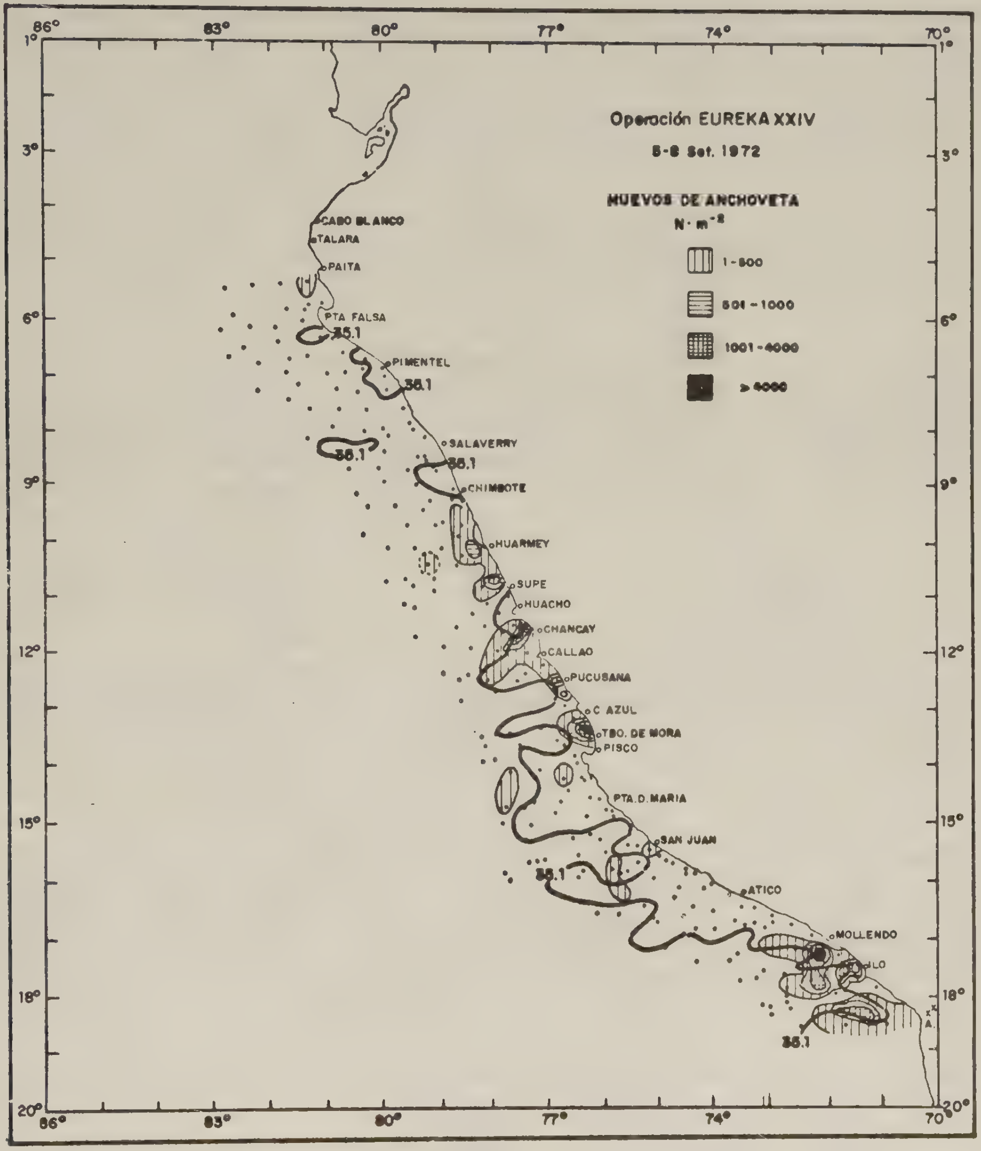

Operación EUREKA XXIV
5-8 Set. 1972
HUEVOS DE ANCHOVETA
N·m⁻²
▥ 1-500
▤ 501-1000
▦ 1001-4000
■ >4000
86°
83°
80°
77°
74°
70°
1°
3°
6°
9°
12°
15°
18°
20°
CABO BLANCO
TALARA
PAITA
PTA FALSA
PIMENTEL
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
C AZUL
TBO. DE MORA
PISCO
PTA.D.MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
35.1

Fig. 13

Fig. 13.- Distribución de huevos de anchoveta en la Operación EUREKA XXIV. 5/8 Septiembre, 1972.

El desove continuó hasta Febrero de 1973, presentándose por primera vez un ciclo de desove totalmente irregular, con máximo en Verano. La irregularidad se repitió en el ciclo siguiente (1973-74) cuando se produjeron pobres desoves en Invierno y un gran desove en Verano de 1974 (Fig. 14).

El Fenómeno "El Niño" 1976, de menor intensidad que el de 1972, se manifestó principalmente con un calentamiento en Enero y Febrero, observado al norte de 15°S, disminuyendo las temperaturas en los siguientes meses, hasta Otoño e inicios de Invierno, donde se reanudaron las altas temperaturas, alcanzando la máxima desviación termal entre Junio y Agosto, asociado con Aguas Subtropicales Superficiales que dominaron gran parte de la costa peruana. Aun cuando a través de observaciones oceanográficas se determinó que estas anomalías ocurrieron durante 10 meses en 1976, las observaciones biológicas mostraron irregularidades desde Diciembre de 1975 durante todo el año 1976 y con consecuencias hasta inicios de 1977 (Santander, 1981 a; Tsukayama y Alvarez, 1981).

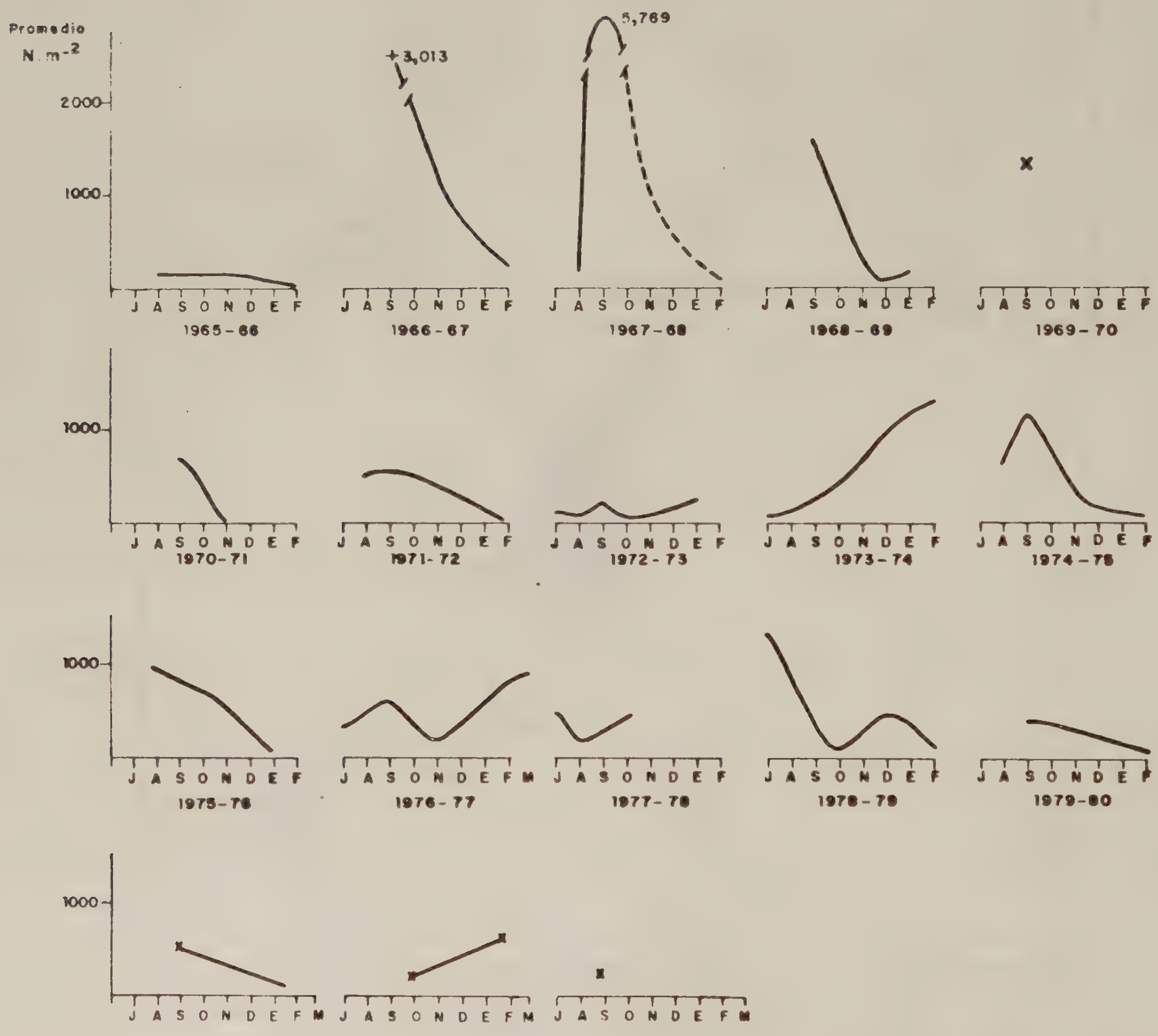


FIG. 14.- CICLOS DE DESOVE DE ANCHOVETA DE 1965 A 1982 EN EL AREA DE 6°-14° L.S.

Con estas condiciones, el desarrollo del ciclo del desove 1976-77 no siguió el patrón normal, observándose una mayor producción del desove en Verano (Fig. 14). En la primera parte del ciclo, Invierno, el desove fue menor al registrado en los de Invierno 1974 y 1975, respectivamente.

Durante el año 1982, antes de la ocurrencia del fenómeno, se registró una estación de Verano fría, con 2° y 3°C por debajo del promedio, principalmente en la parte costera entre 4° y 11°S.

El desove de anchoveta en el norte y centro, fue relativamente intenso, comparados con los Veranos 1979, 1980, e inclusive al de Primavera de 1981 (Fig. 14), obteniéndose un ciclo 1981-82 alterado, con más intenso desove en Verano.

En la estación de Invierno de 1982 (Septiembre) se observaron anomalías térmicas positivas (Fig. 11), con valores de +2°C con respecto al promedio patrón (1928-69). Este calentamiento fue causado por la penetración hasta muy cerca de la costa de aguas sub-tropicales superficiales, con un mayor impacto entre 8° - 13°S, hasta 10 y 20 millas de la costa. El desove de anchoveta se ubicó principalmente al sur de 10°S (Fig. 4). En este período el desove fue menor al observado en el Verano y a los correspondientes de Invierno de los años 1979, 1980 y 1981.

Posteriormente, el calentamiento se ha hecho más intenso, con anomalías positivas por encima de 2° en Octubre, 4° en Noviembre en el área N-C, llegando en Diciembre a 6° en la localidad de Chimbote (09°S). Al sur de Pisco (14°S), las anomalías han sido menores (2° - 4°C).

En el caso de la sardina, desde 1966 hasta 1972, los desoves, fueron muy reducidos (Santander, 1981 a). Desde este año, hasta 1982, el desove se ha venido extendiendo con diferente intensidad a través del tiempo, con tendencia a incrementar hasta 1979, tanto espacialmente, como en densidad (Fig. 6). En los años siguientes, los desoves han venido decreciendo, excepto en Septiembre de 1982, cuando se presentaron las condiciones antes anotadas.

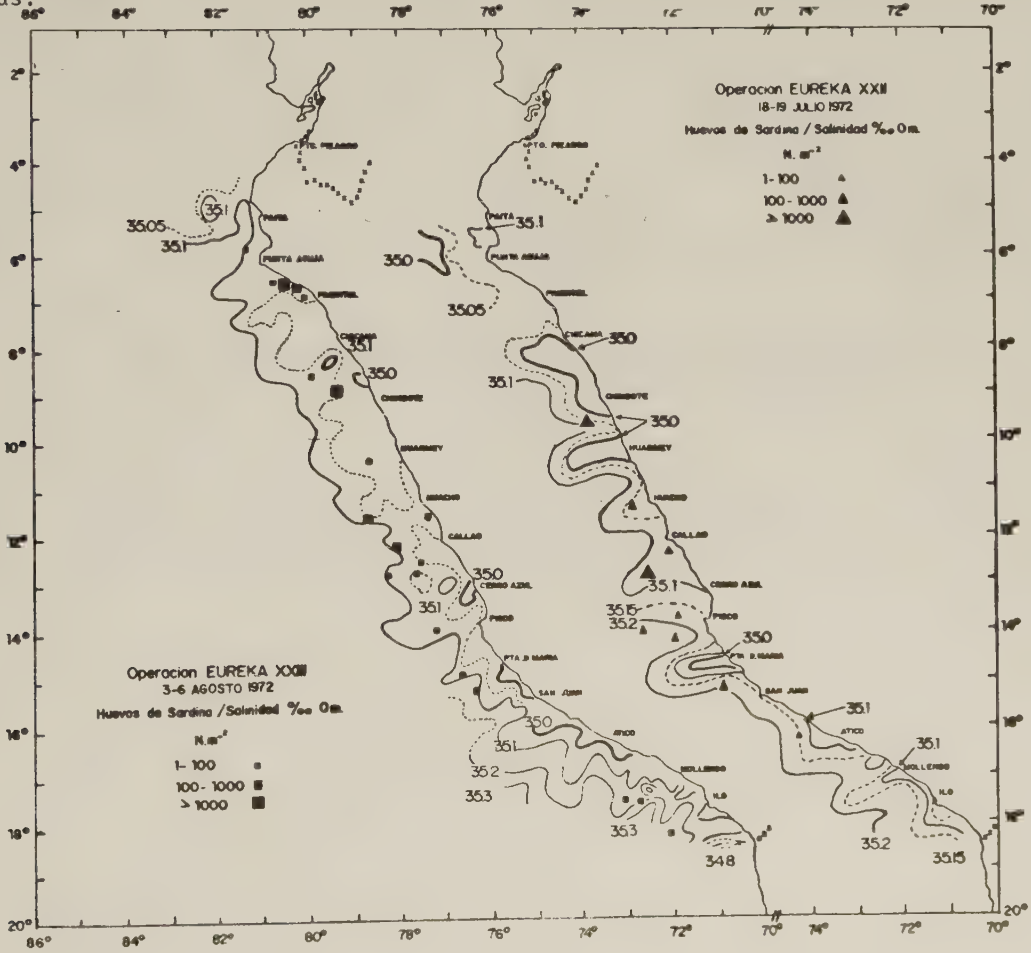

Operacion EUREKA XXII
18-19 JULIO 1972
Huevos de Sardina / Salinidad ‰ 0m.
N. m⁻²
1-100 ▲
100-1000 ▲
≥1000 ▲
Operacion EUREKA XXIII
3-6 AGOSTO 1972
Huevos de Sardina / Salinidad ‰ 0m.
N. m⁻²
1-100 ■
100-1000 ■
≥1000 ■
PAITA
PUNTA AGUJA
PIMENTEL
CHICAMA
CHIMBOTE
HUARMEY
HUACHO
CALLAO
CERRO AZUL
PISCO
SAN JUAN
ATICO
MOLLENDO
ILO
35.05
35.1
35.0
35.15
35.2
35.3
34.8
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 15

Fig. 15.- Distribución de huevos de sardina. Salinidad superficial (o/oo) en la Operación EUREKA XXII. 18/19 Julio, 1972.

Con la ocurrencia del Fenómeno "El Niño" 1972-73, se observó un gran incremento en la distribución del desove y larval, ampliándose su área de distribución a toda la costa. La distribución se localizó en una franja por fuera de las 35 millas de la costa (Fig. 15). Como se ha dicho anteriormente, el pico del desove se produce mayormente al término de la estación de Invierno; pero durante el desarrollo de "El Niño" 1972-73, se produjo un adelanto del máximo en el ciclo del desove hacia el mes de Julio (Fig. 16).

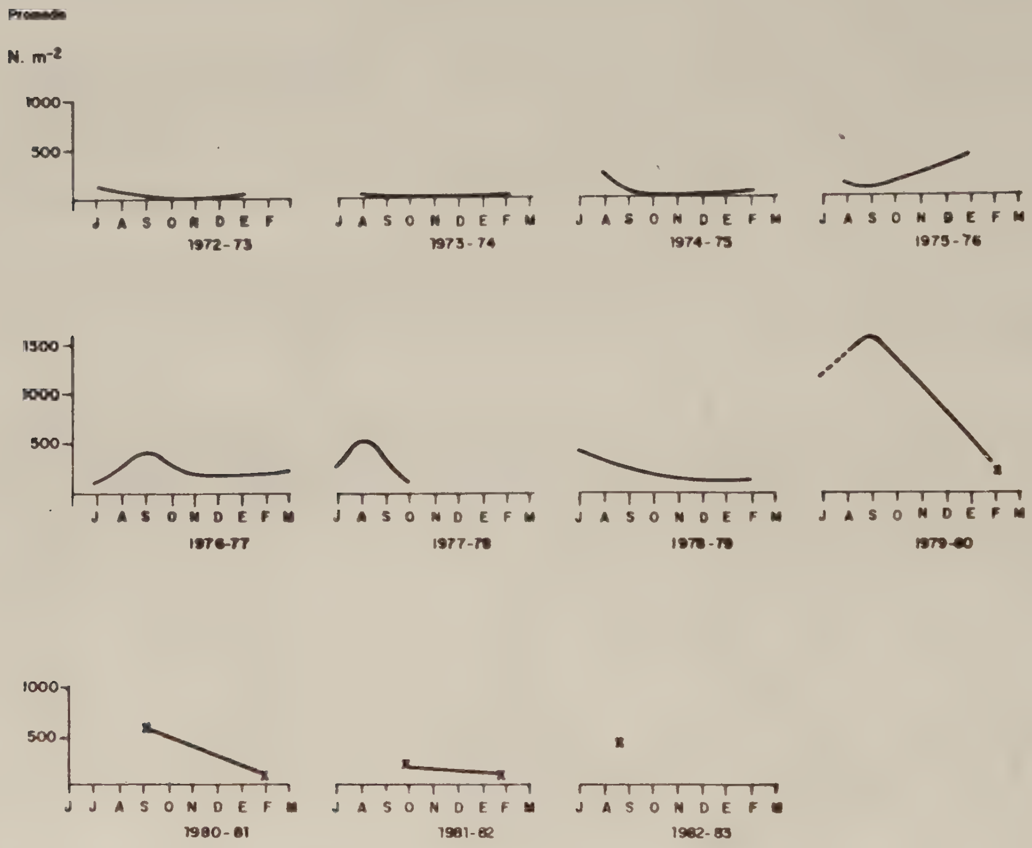


FIG.16.- CICLOS DE DESOVE DE SARDINA DE 1972-1982 EN EL AREA DE 6°-14° L.S.

El efecto del Fenómeno "El Niño" de 1976 en el desove de la sardina fue semejante al observado en 1972 (con una población superior a la de ese año). Después de un año frío (1975), cuando el desove de sardina fue muy escaso, en Agosto de 1976, su distribución se extendió a toda la costa, con densidades superiores a los años anteriores. Durante el ciclo de 1976-1977 el pico del desove se mantuvo en la estación de Invierno (Fig. 16).

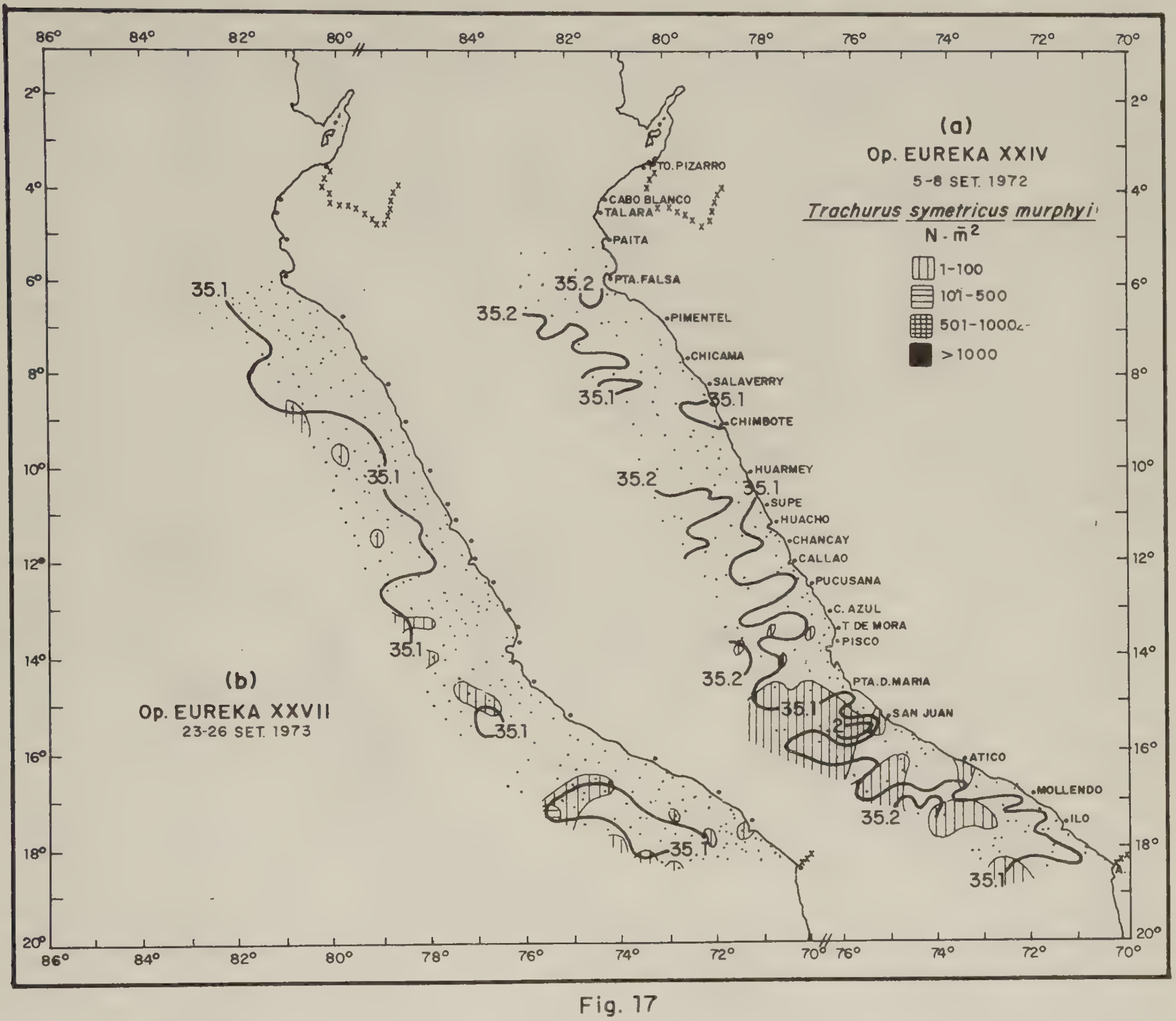

(a)
Op. EUREKA XXIV
5-8 SET. 1972
Trachurus symetricus murphyi
N · m̄²
1-100
101-500
501-1000
>1000
(b)
Op. EUREKA XXVII
23-26 SET. 1973
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
C. AZUL
T DE MORA
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
35.1
35.2
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 17

Fig. 17.- Distribución de larvas de jurel.

(a) En la Operación EUREKA XXIV. 5/8 Septiembre, 1972.
(b) En la Operación EUREKA XXVII. 23/26 Septiembre, 1973.

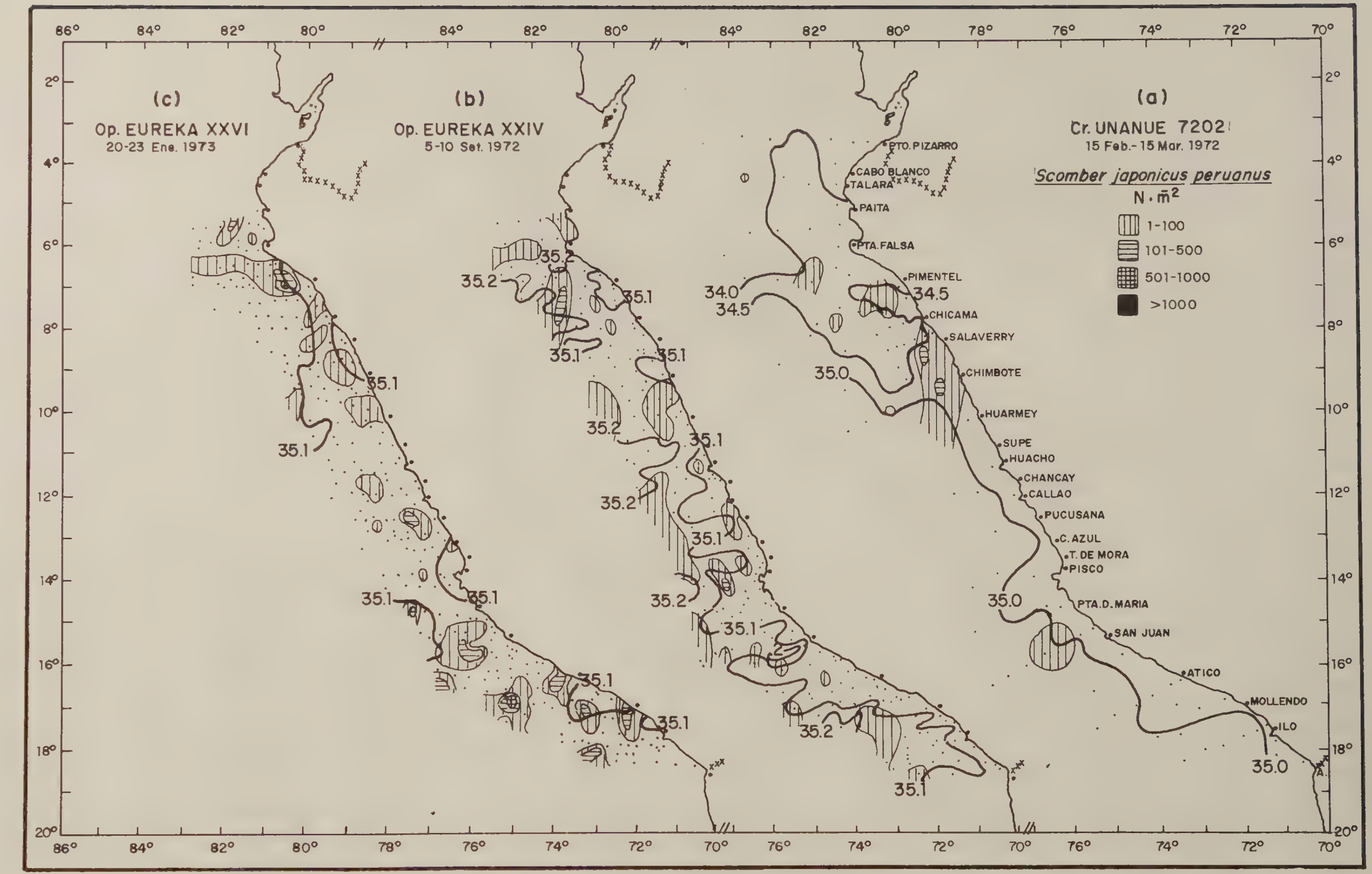

(c)
Op. EUREKA XXVI
20-23 Ene. 1973
(b)
Op. EUREKA XXIV
5-10 Set. 1972
(a)
Cr. UNANUE 7202
15 Feb.-15 Mar. 1972
Scomber japonicus peruanus
N · m̄²
1-100
101-500
501-1000
>1000
PTO. PIZARRO
CABO BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
C. AZUL
T. DE MORA
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
34.0
34.5
35.0
35.1
35.2
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig.18

Fig. 18.- Distribución de larvas de caballa.

(a) En el Crucero 7202. 15 Febrero - 13 Marzo, 1972.
(b) En la Operación EUREKA XXIV. 5/8 Septiembre, 1972
(c) En la Operación EUREKA XXVI. 20/23 Enero, 1973.

En el Verano de 1982, relativamente frío, la distribución del desove de sardina fue muy fraccionado y menor que los encontrados en los veranos de 1979 y 1980. Mientras que en Septiembre del mismo año, el desove de esta especie se extendió amplia y densamente desde 3°30' hasta 8°S; descontinuándose hacia el sur y resultando en un desove superior al encontrado en Verano.

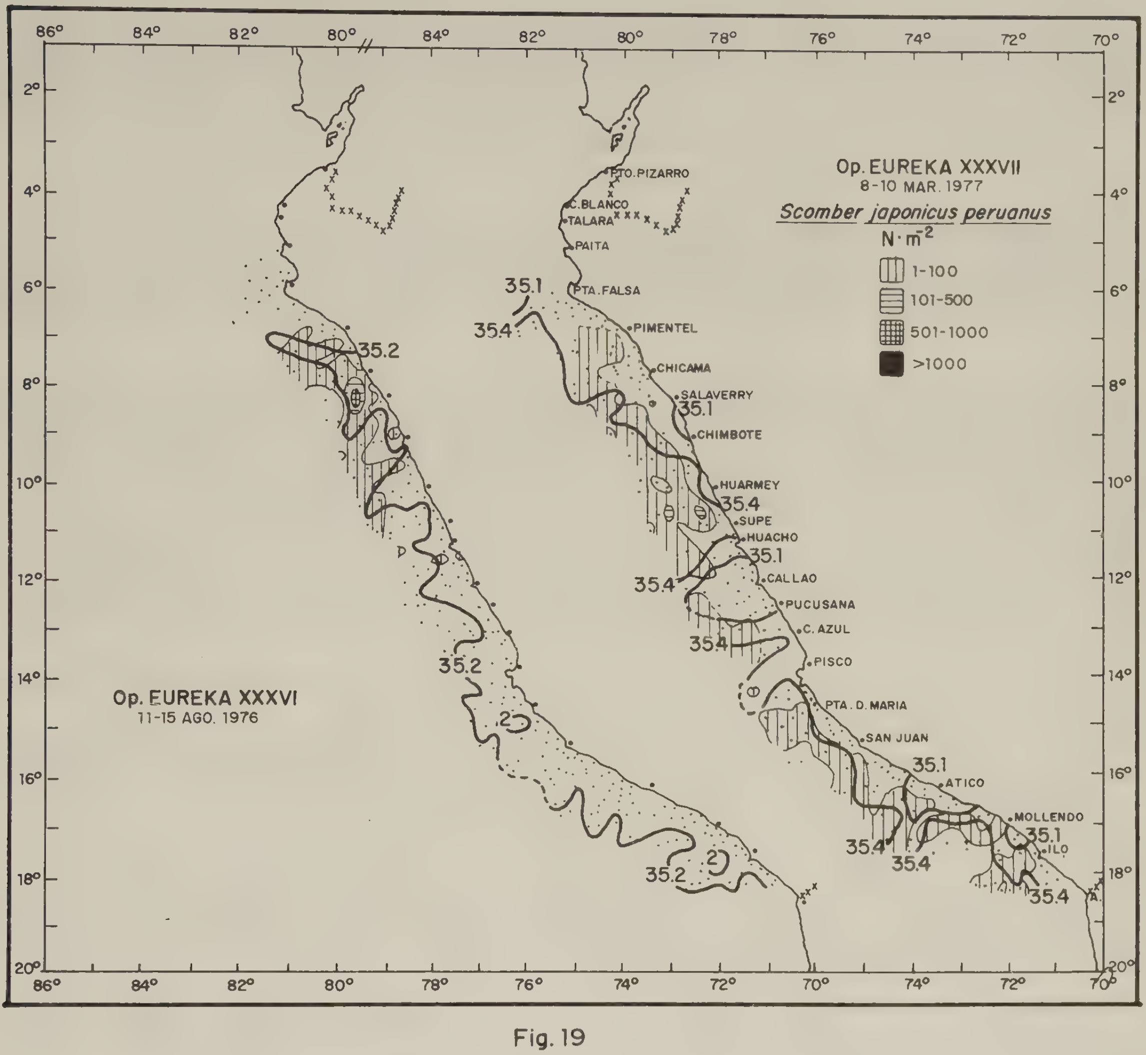

Op. EUREKA XXXVII
8-10 MAR. 1977
Scomber japonicus peruanus
N·m⁻²
▥ 1-100
▤ 101-500
▦ 501-1000
■ >1000
Op. EUREKA XXXVI
11-15 AGO. 1976
PTO. PIZARRO
C. BLANCO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
SALAVERRY
CHIMBOTE
HUARMEY
SUPE
HUACHO
CALLAO
PUCUSANA
C. AZUL
PISCO
PTA. D. MARIA
SAN JUAN
ATICO
MOLLENDO
ILO
35.1
35.2
35.4
86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 19

Fig. 19.- Distribución de larvas de caballa.

(a) En la Operación EUREKA XXXVII. 8/10 Marzo, 1977.
(b) En la Operación EUREKA XXXVI. 11/13 Agosto, 1976.

Como una característica general, los calentamientos de los años "El Niño" 1972 y 1976, afectaron favorablemente los desoves de la sardina (Septiembre), y en los inicios del correspondiente a 1982, los desoves se ven incrementados, con una mayor expansión de sus áreas de distribución, adelantándose sus períodos de desove y sus máximos cuando el calentamiento es de gran intensidad o de efectos prolongados como en 1972, o retrasándose para producir su máximo en Verano cuando las condiciones son frías como en 1975 (Fig. 16).

En concordancia con la distribución larval de jurel, relacionada principalmente con los frentes de Aguas Costeras Frías y Aguas Subtropicales Superficiales los registros obtenidos en los años 1966 a 1968, indican que en Noviembre de 1967 (Primavera), cuando las Aguas Subtropicales Superficiales tuvieron una gran aproximación hacia la costa, la distribución de larvas fue más extensa que en los otros 2 años (Fig. 8). Desde 1972, el número de larvas se ha incrementado principalmente en Septiembre de los años "El Niño" 1972, 1973, y 1976.

Es conveniente hacer notar, que aun cuando estos períodos se denominan "El Niño", las condiciones ambientales no son homógeneas, ni durante todo el año, ni en toda la costa. Particularmente en Septiembre (Invierno) de estos tres años, las condiciones fueron diferentes a la fase de mayor intensidad de el fenómeno, que generalmente es en la estación de Verano.

En Septiembre de 1972, se observó predominio de las Aguas Subtropicales Superficiales en casi toda la costa. En el área sur, el desove de jurel se mostró pararelo con el avance de estas aguas (Fig. 17a). En Septiembre de 1973 cuando el fenómeno ya había finalizado, las Aguas Subtropicales Superficiales se localizaron en algunas áreas al sur de 16°S (Fig. 17b).

Durante 1976, la densidad de las concentraciones fue menor que en los 2 años enumerados. Y en los años intermedios, 1974, 1975 y 1977, la distribución larval fue muy reducida.

Por ser la caballa desovadora de Verano, es la única especie entre estas cuatro, cuyo desove es afectado directamente durante el Fenómeno "El Niño".

La distribución de huevos y larvas, muy dispersa en los veranos de los años 1966 a 1968, se incrementó notablemente en Febrero y Marzo de 1972 (Fig. 18a), principalmente de 6° a 10°S, hasta donde avanzaron las Aguas Ecuatoriales Superficiales.

En Septiembre del mismo año, la distribución larval se extendió a toda la costa, en relación con el avance de las Aguas Subtropicales Superficiales, aun cuando la estación de Invierno no es el período usual de desove (Fig. 18b).

En Enero de 1973, durante la segunda fase de "El Niño", se produjo la máxima densidad larval registrada hasta la fecha, bajo la acción de dos tipos de aguas cálidas. En el Norte hasta 9°S, por el avance de Aguas Ecuatoriales Superficiales y al sur de 15°S, por el acercamiento hacia la costa de Aguas Subtropicales Superficiales.

Las concentraciones en el área sur fueron de mayor densidad que las observadas en el Norte, sugiriendo este tipo de aguas (Subtropicales Superficiales) como las más favorables. (Fig. 18c).

En los años posteriores, las más extensas y densas concentraciones larvales se han producido en los Veranos de 1975, 1977 y 1974 (Fig. 19a) mientras que en los años 1976 y 1982, las concentraciones de Invierno fueron mayores que las de Verano del mismo año. (Fig. 19b), cuando aguas salinas (Aguas Subtropicales Superficiales) dominaron el área de distribución de las larvas.

INTERACCION ENTRE ESPECIES

Los desoves de las cuatro especies enumeradas parecen ubicarse en áreas y períodos de acuerdo a patrones establecidos, que responderían a su estrategia de alimentación y de adaptación a determinadas condiciones ambientales.

En este sentido, las cuatro especies son planctófagas (estadios larvales y juveniles). En estado adulto, la anchoveta y la sardina mantienen este régimen, siendo la sardina preferentemente zooplanctófaga y la anchoveta muestra tener una dieta combinada de fitoplancton y zooplancton (Mendiola, 1978; Alamo, 1981) en relación con la disponibilidad de su alimento en las áreas costeras donde se distribuye esta especie.

El jurel y la caballa adultos, evidenciaban ser mayormente ictiófagos y zooplanctófagos en forma secundaria (Mejía et al., 1970). Sin embargo, durante 1975 y 1977, análisis de contenidos estomacales de caballa, revelan que organismos del zooplancton constituyeron el total de su dieta y en 1976 (Año "El Niño"), su alimento estuvo constituido casi exclusivamente de anchoveta (Sánches, G., comunicación personal), posiblemente por su distribución más costera, favorecida por el avance de Aguas Ecuatoriales Superficiales en Verano y Aguas Subtropicales Superficiales en Invierno.

La distribución de los adultos de estas especies, cubre casi toda la costa peruana; la anchoveta y sardina son más costeras que jurel y caballa, que se encuentran relativamente alejadas de la costa. Sin embargo, en condiciones normales los desoves más importantes ocupan sólo parcialmente el área de distribución de los adultos, estas áreas de desove están delimitadas principalmente, por las Aguas Costeras Frías y las Aguas Subtropicales Superficiales.

De las tres especies desovadoras de Invierno, la anchoveta desova en toda el área costera desde 6°S y hasta 30 millas de la costa aproximadamente, distribución ligada a las Aguas Costeras Frías; la sardina ocupa el área norte-central (03°30' - 15°00'S) por fuera de las 20 millas principalmente colindante con las áreas de la anchoveta, pero con mayor afinidad con las Aguas Subtropicales Superficiales, pudiendo también adaptarse a las Aguas Costeras Frías, y el jurel al sur de 15°S por fuera de las 30 millas de la costa, relacionadas con los frentes de las Aguas Costeras Frías y Aguas Subtropicales Superficiales.

La caballa, la única desovadora de Verano de estas 4 especies, ocurre a lo largo de todo el litoral por fuera de las 20 ó 30 millas de la costa, en aguas subtropicales superficiales, principalmente.

La distribución de las larvas de estas especies, además de tener relación con la distribución de los adultos, parece estar supeditada a las concentraciones de organismos que requieren en su alimentación.

Las larvas de boca grande tienen mayor posibilidad de ingerir presas de mayor tamaño, y aunque las larvas de la anchoveta de California y del Pacific Mackerel (similar a la caballa peruana) tienen aproximadamente el mismo ancho de la boca inicialmente, la del Pacific Mackerel incrementa más rápidamente (Hunter, 1981), con posibilidad de un mayor rango en el tamaño de la presa. Lo que también debe ocurrir con las larvas de jurel y caballa distantes de la costa, en relación con las larvas de sardina y anchoveta, próximas a la costa, donde los organismos de menor tamaño son más abundantes que lejos de la costa.

Las fluctuaciones de las poblaciones de las cuatro especies pelágicas más importantes se reflejan en los cambios de la extensión del área de distribución e intensidad de sus desoves.

Antes de 1972, la anchoveta era el eje principal de este ecosistema y como tal dominaba espacialmente las áreas costeras hasta 60 ú 80 millas de la costa.

Los desoves de anchoveta eran proporcionalmente extensos y los desoves de las otras especies eran limitados.

En 1972, con un reducido nivel poblacional de anchoveta, ocasionado por el intenso esfuerzo de pesca, principalmente de los últimos años de la década del 60 y la ocurrencia del Fenómeno "El Niño" derivó en la reducción de la distribución de la anchoveta. Al mismo tiempo, especies como la sardina, evidenciaron que su población se incrementaba por las altas capturas registradas desde 1973 (132 mil toneladas) y entre 1978 y 1981 (1.4 millones de toneladas en promedio), Tsukayama (en prensa).

Al igual que la sardina, las poblaciones de jurel y caballa también parecen haber aumentado lo que a falta de evaluaciones se ha puesto en evidencia por el aumento de sus capturas.

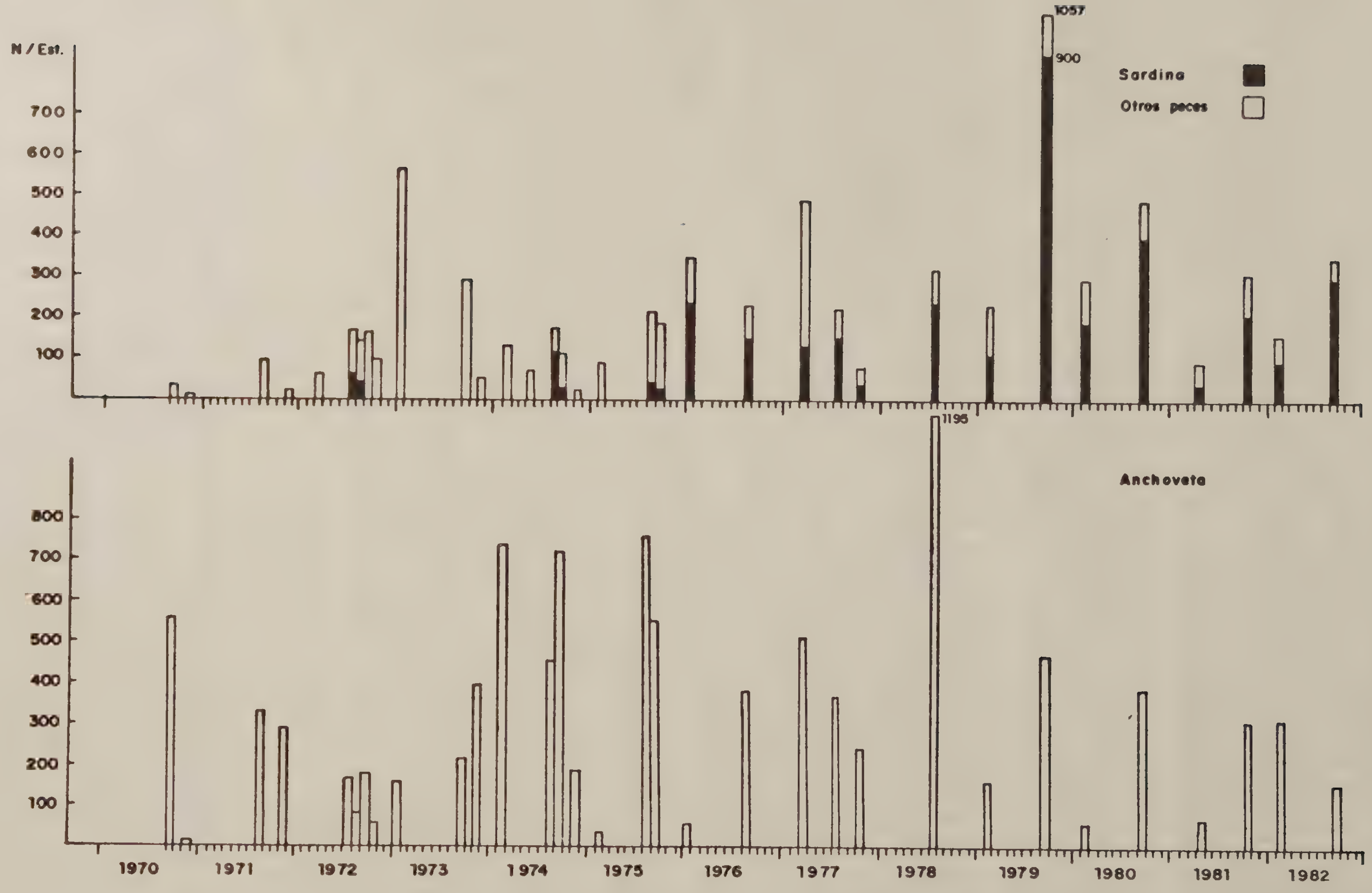


Fig. 20.- Composición del ictioplancton en el área de 04°00' a 18°00'S.

Pararelamente, la composición del ictioplancton desde 1961 mostró cambios concordantes con las fluctuaciones de las poblaciones. De 1961 a 1971, los huevos de anchoveta fluctuaron entre 80 y 90%, excepto en 1965 que descendió a 65% en un año de anomalías moderadas. En 1972-1973, los huevos de anchoveta constituyeron alrededor del 50% (Santander, 1981b). Desde 1974 a la fecha, las proporciones son fluctuantes tendientes al decrecimiento (Fig. 20).

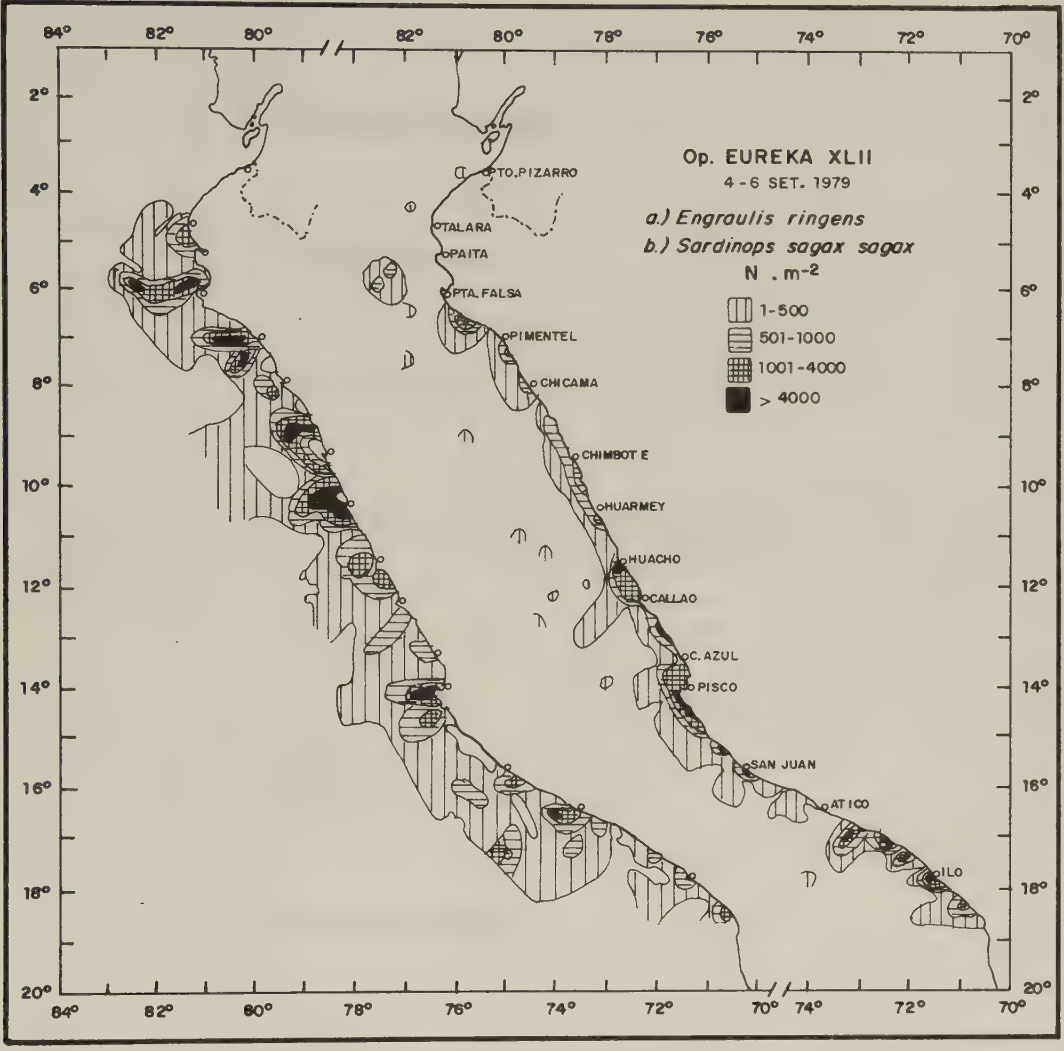

Op. EUREKA XLII
4 - 6 SET. 1979
a.) Engraulis ringens
b.) Sardinops sagax sagax
N . m-2
1-500
501-1000
1001-4000
> 4000
PTO. PIZARRO
TALARA
PAITA
PTA. FALSA
PIMENTEL
CHICAMA
CHIMBOTE
HUARMEY
HUACHO
CALLAO
C. AZUL
PISCO
SAN JUAN
ATICO
ILO
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°

Fig. 21

Fig. 21.- Distribución de huevos de sardina en la Operación EUREKA XLII. 4/6 Septiembre, 1979.

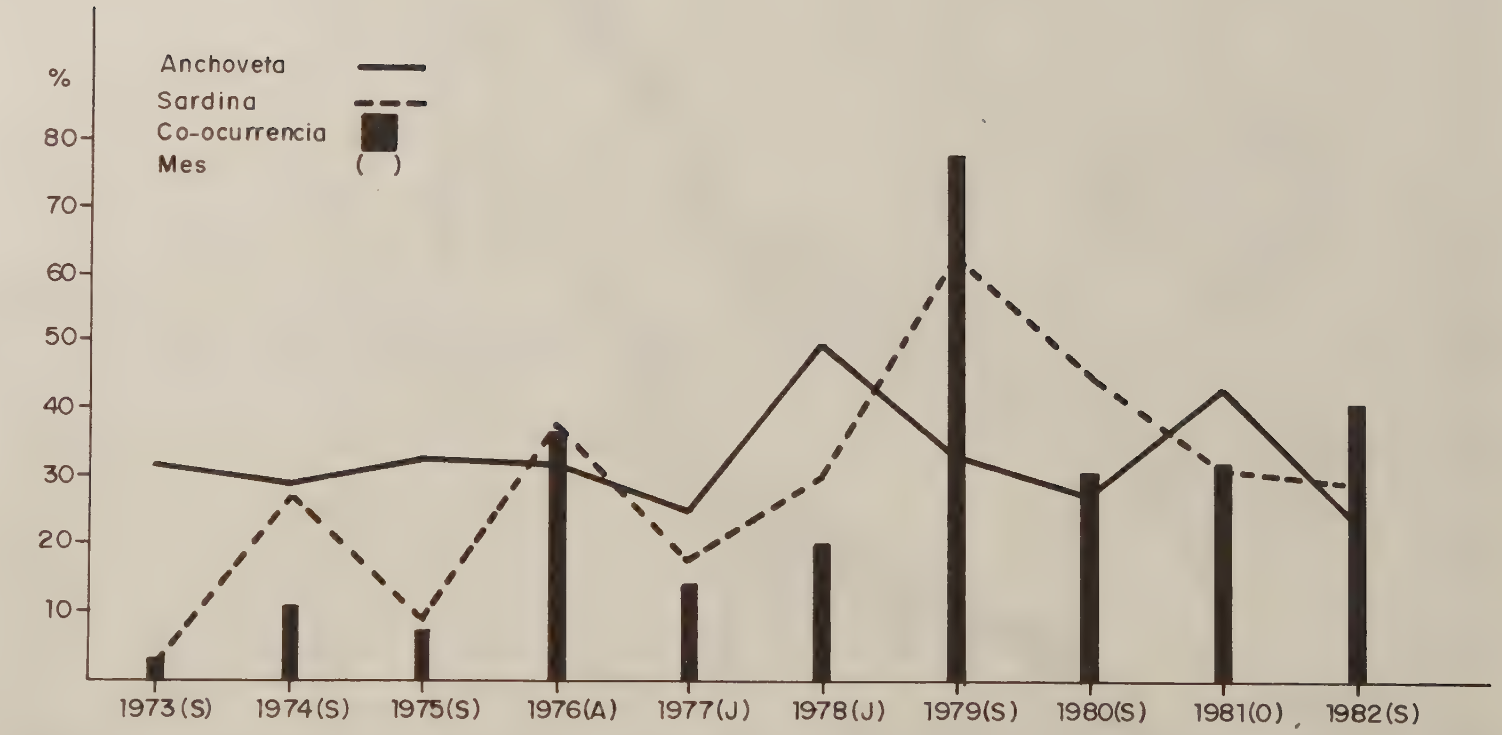


Fig. 22.- Frecuencia y Co ocurrencia de desoves de Anchoveta y Sardina de 1973 a 1982 (Invierno)

Al nivel de ictioplancton, las interacciones parecen ser más directas entre la anchoveta y sardina, principalmente desde 1972. La reducción de las áreas de desove que se venían produciendo desde 1968, 1969 y el desplazamiento hacia el sur por las condiciones anómalas de 1972-1973, permitieron la aproximación de las áreas de desove de sardina hacia la costa, ocupando parcialmente el área de desove de anchoveta. En los años subsiguientes, los leves incrementos iniciales (1974-1975) y mayores de 1976 a 1979 (Fig. 21) fueron aparejados con una mayor extensión de sus áreas de desove y su contínuo y gradual avance en la ocupación de las áreas de desove de anchoveta (Fig. 22). De 1980 a 1982 los índices de desove, sugieren que también la población de sardina está decreciendo, con ligeros incrementos, cuando se producen calentamientos como el observado en Septiembre de 1982 (Fig. 16). La reducción de estos desoves no implica necesariamente una menor ocupación de las áreas de anchoveta pero si se observa una menor co-ocurrencia de las áreas de desove, posiblemente debido a la reducción de las áreas de desove de anchoveta y a los desplazamientos hacia el sur.

La sobreposición de las áreas de desove de estas especies, generalmente se presenta en los bordes de ambas y los principales focos de desoves no son co-ocurrentes.

Una consecuencia de la ocupación de áreas comunes para desovar, parece ser el del aumento de la predación sobre huevos y larvas de anchoveta, que se adiciona al producido por el de sus progenitores. El número promedio de huevos de anchoveta en estómagos de sardina, en Septiembre de 1981, fue el triple del hallado en estómagos de anchoveta (Santander et al., este volumen), que como efecto concomitante debe influir en la falla de los reclutamientos de los 2 últimos años.

Además de la predación mutua de los adultos sobre huevos y larvas, esta interacción se debe intensificar por la posible competencia por alimentación de estas dos especies en sus diferentes fases de vida, y de la caballa cuando ocurren avances de las Aguas Subtropicales Superficiales que favorecen la ampliación de su distribución hacia la costa. Sin embargo, el pico del período de desove de la caballa no es coincidente con los de las otras 2 especies, y el efecto debe ser menor a nivel de fases larvales.

Información preliminar sobre predación de caballa, sobre huevos de anchoveta y sardina en la localidad de Chimbote (09ºS) de 1979 a 1981, muestra que hay una mayor proporción de huevos de sardina en sus contenidos estomacales (Miñano, Com.pers) debido probablemente a una mayor relación distribucional con esta especie.

Las interacciones de estas tres especies con el jurel en el ictioplancton, parecen ser menores por la ubicación espacial del desove, no compartida con anchoveta, ni sardina; ni en el tiempo con la caballa.

Nuestros resultados indican que los incrementos en las concentraciones larvales son reducidas y no son comparables a los de caballa, ni mucho menos a los de sardina.

Una causa atribuible a esta diferencia, puede deberse a un patrón de desove menos intenso, observado por Hewitt (1981) para *Trachurus symmetricus* de California, a la gran velocidad de natación y a la habilidad de evitamiento, comparada con las larvas de Clupeidae (Lenartz, 1973).

DISCUSION

El conjunto de anomalías conocidas como fenómeno "El Niño" tienen efectos muy variables en el ambiente marino, se presentan en períodos de tiempo irregulares, con diferente intensidad y donde interactúan procesos físico-químicos y biológicos muy variables, y afectan en diferente grado los huevos y larvas de peces pelágicos, particularmente a las especies, anchoveta, sardina, caballa y jurel. Alteran el proceso reproductivo de los adultos, cambiando los patrones de desove y de distribución larval.

Los fenómenos "El Niño" observados en 1965, 1972-73 y 1976, frente al Perú tienen como característica común, en la capa superficial donde se distribuyen estas especies, la transgresión de las Aguas Ecuatoriales Superficiales hacia el sur y de las Aguas Subtropicales Superficiales hacia la costa, reduciendo en su avance los afloramientos costeros.

En el caso de la anchoveta, reducen la intensidad del desove, concentran los desoves en áreas muy próximas a la costa y cuando las condiciones son extremas, desplazan estas áreas hacia el sur, donde el efecto de estas anomalías parecen ser menores.

Hasta 1971, en condiciones normales los desoves en el área sur de 14°S eran muy esporádicos. En los últimos 10 años se están haciendo más frecuentes con los efectos consiguientes de la colonización de una región de intenso afloramiento, donde los eventos de los vientos, la variabilidad termal y los procesos de mezcla, son mayores. A diferencia de la estabilidad de los procesos de afloramiento y baja turbulencia del área norte-central (6° - 14°S). Según Shaffer (1982), una celda de afloramiento con posibilidades de recirculación de agua en la capa superficial en las proximidades de 9°S, sería la causante de la regeneración de nutrientes y materia orgánica y en consecuencia de la alta productividad del área. Esta celda localizada también entre 4° y 6°S, estaría asociada con un flujo sub-superficial hacia el sur, que según Brockmann et al., (1980) hasta 10°S se localiza sobre la plataforma y al sur de 12° y 15°S, se ubica además sobre el talud, debilitándose en su recorrido hacia el sur.

Desde 1972, esta área norte-central es compartida para el desove y distribución larval con la sardina y aunque esta especie se extiende también hacia el norte y hacia afuera de la costa para desovar, sus mayores concentraciones se sitúan entre 5° y 12°S.

Estas dos especies desovan en el mismo período (Julio-Marzo) y co-ocurren parcialmente en los bordes de sus áreas de desove, más no en sus focos de desove, habiendo llegado como máximo a ocupar la sardina el 78% del área de desove de anchoveta, en Septiembre de 1979. Año en el que se registraron las mayores capturas de sardina (1.7 millones de toneladas; Tsukayama, en prensa), concordante posiblemente con el máximo nivel de esta población en los últimos años.

La ocupación de áreas de desove comunes, conlleva a una mayor interacción entre estas dos especies planctófagas: de competencia entre larvas de las dos especies y entre adultos al momento del desove y de predacción de adultos sobre huevos y larvas, entre especies.

En condiciones normales los picos de desove de estas dos especies se producen a fines de invierno, aparentemente ligados a los máximos de fitoplancton y zooplancton de los ciclos de producción anual. Con la ocurrencia del fenómeno "El Niño" en los años 1972-73 y 1976, este patrón del desove de anchoveta se alteró produciéndose un pobre desove durante el ciclo y desplazándose el máximo hacia verano (Ciclos: 1972-73; 1973-74 y 1976-77).

En la sardina la traslación del pico del desove es menos diferenciado en los años "El Niño". Solamente en 1972, se observó un adelanto del pico del desove, notándose más bien un incremento en la abundancia del desove y una mayor expansión de sus áreas, cada vez que ocurre un fenómeno "El Niño".

La mayor intensidad y extensión del desove de sardina parece ser una consecuencia del dominio de las Aguas Subtropicales Superficiales, o de los procesos de mezcla de éstas con las Aguas Ecuatoriales Superficiales, más que del avance de éstas; pues durante los años "El Niño" la mayor intensidad del fenómeno se da en verano, suavizándose lo riguroso de las condiciones de las Aguas Ecuatoriales Superficiales en invierno, cuando generalmente dominan las Aguas Subtropicales Superficiales y los procesos de mezcla de la columna vertical.

Cuando se iniciaron los incrementos sustanciales de sardina en los años 1972, 1973 y 1974, la mayor intensidad del desove se producía en invierno, pero anterior al máximo de anchoveta. Pudiendo por este hecho haber sido favorecida la sobrevivencia de las larvas de sardina. Walsh et al., (1980) sugieren que cuando las larvas de ambas especies tienen que competir, durante "El Niño" por el mismo alimento, por adelanto en el tiempo de desove es posible que la sobrevivencia de sus larvas se beneficie. Después de 1976, los picos de desove de anchoveta y sardina parecen coincidir en el tiempo con más frecuencia que previamente; lo que incidiría en una mayor competencia.

Tanto la sobreposición de sus áreas de desove, como la coincidencia de los picos de desove y el cada vez más frecuente acercamiento de las Aguas Subtropicales Superficiales, en época de desove, limitan la distribución de las áreas de desove y larval de anchoveta. Usualmente la distribución de larvas ocupa una mayor extensión que la del desove, como efecto de la dinámica del agua, distribuyendo a las larvas en un área mayor por la diferencia en el tiempo de duración del estadio de huevo (alrededor de dos días), con el de larvas (de 20 a 50 días; Smith, 1981). Hasta 1971 el área de distribución larval era mayor que la de huevos; desde este año y posteriormente en 1972, 1976, 1977, 1980, 1981 y 1982, se ha observado que la extensión larval es menor que la extensión del desove, suponiéndose que se debe a una mayor mortalidad de huevos y/o larvas; o a la existencia de un patrón de circulación que las mantiene en áreas más próximas a la costa. Sin embargo, esta última posibilidad significaría un aumento en la densidad larval, lo cual no ha sido observado. Por lo que es más probable que una mayor mortalidad esté ocurriendo en los últimos años.

El jurel, siendo desovadora de invierno, no tiene mayor interacción con los desoves de anchoveta y sardina, por ocupar diferente área de desove, que las más importantes de anchoveta y sardina. Pero se supone que algún tipo de interacción se está produciendo en el área sur, donde en los últimos años se han registrado desoves de anchoveta; principalmente por una mayor aproximación del jurel cuando las Aguas Subtropicales Superficiales tienen un mayor acercamiento hacia la costa.

La caballa por ser desovadora de verano, en condiciones normales, localiza sus desoves por fuera de las áreas de desove de Verano de anchoveta y sardina.

El nivel de predación sobre anchoveta adulta ha disminuido y en su lugar el zooplancton parece ser el principal componente de su alimento. Pero en condiciones "El Niño", además de predar sobre la anchoveta y sardina por un mayor acercamiento hacia la costa, los desoves de caballa se incrementan, sus áreas de desove son más cercanas a la costa e inclusive se reproduce durante la estación de Invierno.

La triple co-ocurrencia del desove de caballa, anchoveta y sardina en estos períodos es evidenciada también por la predación de la caballa adulta sobre huevos de anchoveta y sardina, siendo mayor sobre esta segunda especie, por una mayor relación en la distribución.

Los decrementos sucesivos de la población de anchoveta que se venían produciendo desde antes del Fenómeno "El Niño" 1972-73, por la creciente presión pesquera y los últimos tres Fenómenos "El Niño" experimentados, han afectado profundamente a esta población a través del proceso reproductivo y las subsecuentes fases de huevos y larvas.

En contraposición, las otras tres especies pelágicas, sardina, jurel y caballa, han evidenciado incrementos sustanciales a partir de la declinación del stock de anchoveta y de los cambios ambientales que favorecen la ampliación de las áreas de desove y larval y posiblemente de una mayor sobrevivencia de huevos y larvas.

REFERENCIAS

Alamo, A. 1981. Estudio sobre la alimentación de la anchoveta peruana Engraulis ringens J. durante los años 1976 y 1977. Bol.Inst.Mar. Péru-Callao. Vol.Extraord. pp. 258-268.

Brockmann, C.E., E. Fahrbach, A. Huyer, and R.L. Smith. 1980. The poleward undercurrent along the Peru coast: 5º to 15ºS. Deep-Sea Res. 27A:847-856.

De Vries, T.J. and W.G. Pearcy. 1980. Fish debris in sediments of the upwelling zone off Central Peru: A late quaternary record. Deep-Sea Res. 28(1A):87-109.

Guillén, O. y R. Calienes. 1981. Upwelling off Chimbote. pp. 312-326. In Coastal Upwelling. (F.A. Richards, ed.). American Geophysical Union, Washington, D.C.

Hewitt, R.P. 1981. The value of pattern in the distribution of young fish. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:229-236.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. pp. 33-77. In Marine Fish Larvae. Morphology, Ecology and Relation to Fisheries. (R. Lasker, ed.). Washington Sea Grant Program, University of Washington Press, Seattle and London.

Lenarz, W.H. 1973. Dependence of catch rates on size of fish larvae. Rapp.P.-v.-Réun.Cons.int.Explor.Mer. 164:270-275.

Mejía, J., M. Samamé y A. Pastor. 1970. Información básica de los principales peces de consumo. Serie Informes Especiales Inst.Mar Perú-Callao. 62:1-28.

Mendiola, B.R. 1978. El alimento de la anchoveta Engraulis ringens J. en un área de afloramineto (San Juan). Informe Inst.Mar Perú-Callao. No. 49. pp. 1-16.

Mendiola, B. y N. Ochoa. 1980. Phytoplankton and spawning of anchoveta. pp. 241-253. In IOC Workshop Report No. 28 (G.D. Sharp, ed.). IOC/UNESCO, Paris.

Santander, H. 1974. Cosecha estable del zooplancton. Serie Informes Especiales Inst.Mar Perú-Callao. 148:1-15.

____________. 1981a. Patrones de distribución y fluctuaciones de desoves de anchoveta y sardina. Bol.Inst.Mar. Perú-Callao. Vol.Extraord. pp. 180-192.

____________. 1981b. Fluctuaciones del desove de anchoveta y algunos factores relacionados. pp. 255-274. En IOC Workshop Report. No. 28 (G.D. Sharp, ed.). IOC/UNESCO, Paris.

Santander, H., J. Alheit, A.D. MacCall y A. Alamo. (Este volumen). Egg mortality of the Peruvian anchovy (Engraulis ringens) caused by cannibalism and predation by sardines (Sardinops sagax).

Shaffer, G. 1982. On the upwelling circulation over the wide shelf off Peru: 1. circulation. J.Mar.Res. 40(2):293-314.

Smith, P. 1981. Fisheries on coastal pelagic schooling fish. pp. 2-31. In Marine Fish Larvae. Morphology, Ecology and Relation to Fisheries (R. Lasker, ed.) Washington Sea Grant Program, University of Washington Press, Seattle and London.

Tsukayama, I. En prensa. Recursos pelágicos y sus pesquerías en el Perú. X Reunión de COCIC. Guayaquil, 25-29 Oct. 1982.

Tsukayama, I. y M.A. Alvarez. 1981. Fluctuaciones en el stock de anchovetas desovantes durante las temporadas reproductoras de primavera 1964-1978. pp. 233-240. En IOC Workshop Report No. 28 (G.D. Sharp, ed.) IOC/UNESCO, Paris.

Walsh, J.J., T.E. Whitledge, W.E. Esias, R.L. Smith, S.A. Huntsman, H. Santander and B.R. de Mendiola. 1980. The spawning habitat of the Peruvian anchovy, Engraulis ringens. Deep-Sea Res. 27A:1-28.

Ware, D., B.R. de Mendiola and D.S. Newhouse. 1980. Behaviour of first feeding Peruvian anchoveta largae Engraulis ringens. pp. 467-474. In Symposium on Early Life History of Fish (K. Sherman and G. Hempel, eds.). Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178.

Zuta, S. y O. Guillén. 1970. Oceanografía de las aguas costeras del Péru. Bol.Inst.Mar. Perú-Callao 2(5):157-324.

Zuta, S., T. Rivera y A. Bustamante. 1978. Hydrographic aspects of the main upwelling areas of Peru. pp. 235-257. In Upwelling Ecosystems. (R. Boje and M. Tomczak, eds.).

Zuta, S., J. Valdivia, D. Enfield y P. Lagos. 1976. Aspectos físicos del Fenómeno "El Niño". Guayaquil, Ecuador. 4-12 Dic. 1974. pp. 3-61.

PART III - IMPACTS OF ENVIRONMENTAL AND RESOURCES VARIABILITY ON HUMAN COMMUNITIES

PARTE III - REPERCUSIONES DE LA VARIABILIDAD DEL AMBIENTE Y DE LOS RECURSOS EN LAS COMUNIDADES HUMANAS

MAN, STATE, AND FISHERIES:

AN INQUIRY INTO SOME SOCIETAL CONSTRAINTS THAT AFFECT FISHERIES MANAGEMENT

by

M.H. Glantz

Head, Environmental and Societal Impacts Group
National Center for Atmospheric Research*
Boulder, CO 80307, USA

---

* The National Center for Atmospheric Research is sponsored by the National Science Foundation.

Resumen

La pesca no es solo una actividad económica, es también una actividad política, cultural y social. Desde esta perspectiva se identifican algunos de los factores que afectan la implementación de estrategias racionales de ordenación de la explotación de los recursos marinos renovables. Se analizan los diversos factores que influenciaron la explotación de la anchoveta peruana con la finalidad de aplicar estas experiencias en la ordenación de otras pesquerías. Los éxitos y fracasos de la ordenación de la pesca están relacionados con actividades al nivel internacional, al comportamiento de grupos a nivel nacional, y al comportamiento a nivel individual. En este documento se tratan estos tres niveles como categorías de factores distintos que afectan la ordenación pesquera.

INTRODUCTION

Rational fisheries management strategies must compete with a broad spectrum of societal factors that influence the exploitation of marine resources. Fishing is not only an economic activity, but political, cultural, and social as well. Therefore, to understand how a particular fishery has been managed requires investigations by social as well as physical scientists.

The purpose of this paper is to identify some of these factors that might impinge on the implementation of rational management strategies for living marine resources. The focus of this paper will be on pelagic fish in general and the Peruvian anchoveta fishery in particular. This fishery underwent rapid growth and development, beginning in the early 1950's, and its history is relatively well documented. The Peruvian anchoveta fishery shares some marine biological as well as oceanographic and climatological characteristics with other eastern boundary current fisheries (e.g., Parrish et al., 1983; Troadec et al., 1980). In addition, Peru shares some fisheries management characteristics with other coastal countries that exploit their eastern boundary current fisheries.

Pelagic fish dwell near the surface of the ocean, have high rates of natural mortality, have a highly aggregated distribution, are shoaling forage fish, and are apparently extremely vulnerable to subtle as well as drastic variations in their atmospheric and marine environments. Shoaling pelagic fish are relatively easy to capture with efficient gear and large quantities can be taken in a short period of time. While some species are used as food fish, they are also of commercial value for reduction to fishmeal. Their value as fishmeal stems more from the tonnage of landings than from their value per unit of fish. Fishmeal is used as a feed supplement, primarily for poultry and livestock. It may be produced from whole fish and other marine organisms not used for human consumption, from by-catches or surplus catches obtained from catches for human consumption, or from fish offals obtained during the processing of fish (Popiel and Sosinski, 1973).

Fish populations in general have characteristics that set them apart from other living resources. Therefore, analogies made with forests, soils, and renewable resources in general, that sometimes appear in the literature, must be used with great care (e.g., Clark, 1981). Within the fish populations there are species and subspecies which can be set apart from each other according to specific characteristic differences. Careful comparisons between similar species can be a fruitful approach to understanding similar stocks in different regions where some information exists for one region but is available to a lesser extent for other regions. In the absence of perfect information about any single fish stock or fishery, the use of the comparisons for the purpose of identifying analogies can provide valuable insights into the management of fisheries based on similar stocks (Bakun, et al., 1982; Troadec et al., 1980).

One can find views throughout the fisheries (and more broadly, resource) management literature that relate the successes and failures of renewable resource management to either activities at the international level ("international demands for fishmeal in combination with Peruvian import restrictions sparked the Peruvian production of fishing boats"), group behaviour at the national level ("if you allow an industrial fishery to begin, it will destroy the guano resource"), or individual behaviour ("fishermen want to sink every other boat but their own").

The framework used in this paper treats these three levels of analysis (the international, the state, and the individual) as three distinct categories of factors that can affect the management of a fishery. By separating these three levels for analytical purposes, such a framework encourages a broader consideration of potentially relevant factors for managing a fishery than just the consideration of fish population dynamics or oceanographic variables that are known to affect marine life. This approach could lead to the identification of factors that affect management strategies for the Peruvian anchoveta fishery in particular and for other eastern boundary current pelagic fisheries in general. If deemed useful in these instances, such a framework for analysis might be used to identify societal and other factors that might enhance or constrain the management strategies for other fisheries as well.

As the reader will see, it is not always easy to classify events as falling exclusively in one of the three levels. In fact, some of the events discussed may appear in more than one of the three levels of analysis. One such example relates to the rapid growth of Peru's exports and whether it was because of international level or national level causes. As Roemer (1970, p. 45) put it, "To what extent was Peru merely the passive beneficiary of expanding markets and to what extent did it become a more efficient producer of its export products than its competition?" The categories in which to discuss different events or activities were selected by the author according to his perceptions about which level was most appropriate.

There are several important areas not addressed in this paper because they have already received widespread attention in the fisheries literature. These include the competition of economic models for the attention of (and use by) fishery managers, the strengths and weaknesses of different competing fish population models, and detailed considerations of marketing factors that can affect how a fishery might be managed. Also omitted are discussions of the numerous regulatory schemes that have been implemented or have been proposed for implementation in attempts at rational fishery management. In addition, the paper presents examples drawn only from coastal pelagic fisheries, so as to avoid selective use of examples from different types of living marine resources (crustaceans, demersals, whales, shellfish, ocean pelagic, and so forth) in order to make a point. This type of selective attention is often misleading to policymakers, because, as one might effectively argue, different species require different management schemes.

Finally, this paper is not an attempt to present new factual information on fisheries and their management, but to present a new way of organizing and evaluating existing information. It is the application of an existing framework for analysis (Waltz, 1959) to better understand the different influences, stimuli, and constraints that affect the management of a living marine resource such as the Peruvian anchoveta.

Peru: An Introduction

Peru has traditionally been divided into three geographically defined zones; the coastal plain, occupied to a large extent by coastal deserts, the mountainous sierra, and the jungle or selva (Miller *et al.*, 1974, p. 7). This view of Peru persists today (e.g., Banks and Overstreet, 1981, p. 2981). In the mid-1970's, however, a Peruvian geographer challenged the traditional division into three regions. He divided Peru into eight geographically defined regions (Pulgar Vidal, n.d.). Like other geographical accounts, however, this textbook also combined the sea with the coastal plain. In fact, little attention was devoted to consideration of the coastal marine environment.

In a conference report on Social and Economic Change in Peru (Miller *et al.*, 1974, p. 7), the conventional division of Peru into three parts was also challenged. The editors of this report suggested that there be a different emphasis, other than geography, based on

> ...functional links rather than characteristics of terrain, land-use and society. The concept of functional regions underlies the modern division of Peru into planning regions ...which transcend environmental contrasts, brutal and striking though they are.

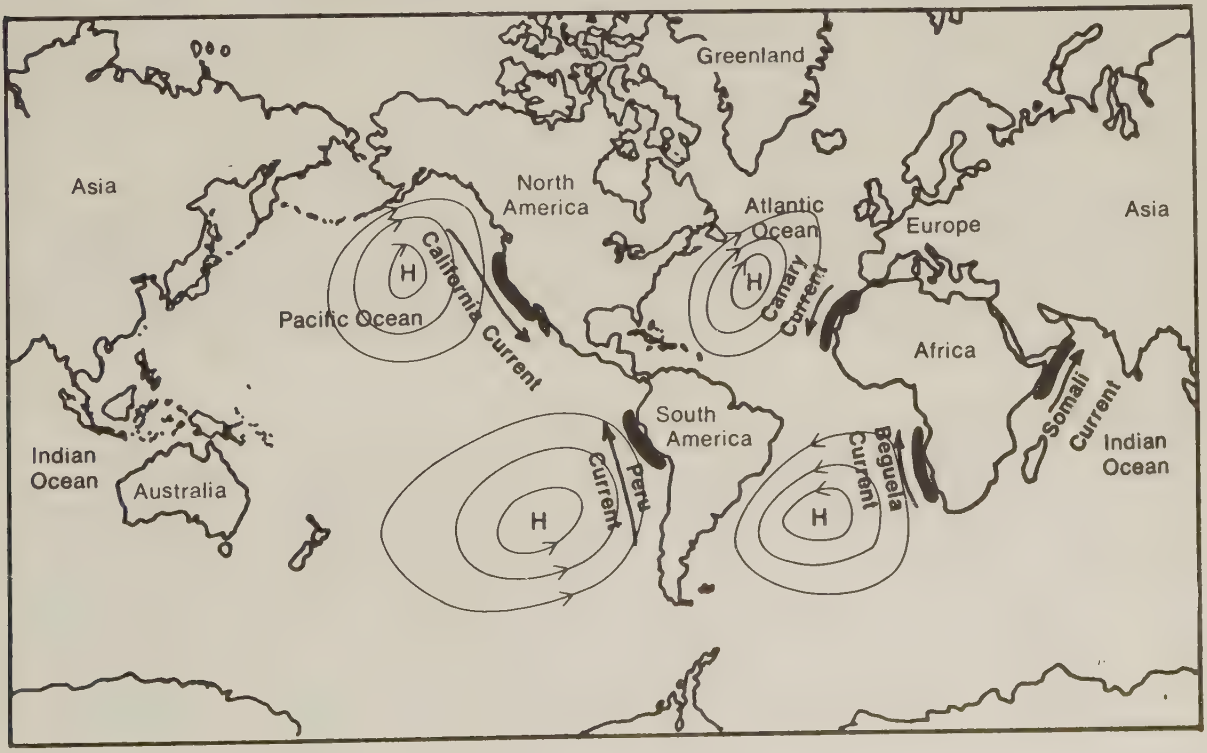
The examples given at this particular conference centered on mining and agriculture, suggesting, for example, that the cotton production on coastal estates had ties to the interior for labor and to Lima (Peru's capital) for transportation but little interaction with other regions of Peru. This particular conference had little discussion of Peru's living marine resources. These few examples, together with other evidence, suggest a traditional bias in Peru toward the land and its resources (e.g., minerals, and food and fiber crops), despite the importance to that country of coastal living marine resources. This bias toward the land has probably affected how Peru's marine resources have been viewed.

Given the conventional division of countries according to their geophysical features, and given the rich biological productivity of the Peruvian coastal waters and the importance of those waters to the Peruvian economy, and given that its geophysical features are distinct from the geophysical features of other terrestrial regions of Peru, Peru's coastal waters could (if not should) have been separated as yet another (ninth) distinct geographical region. Reinforcing this contention, Peru's controversial Fishing Minister under General Velasco (1968-1975), Tantalēan, established a new slogan, "La Marcha Hacia el Oeste" ("The march to the west," that is, to the ocean). He also noted that "Peru needed to awaken its maritime consciousness" (Tantalēan, 1978, p. 214).

One of the most productive upwelling regions in the world in terms of primary productivity is along the coast of Peru (e.g., Smith, 1968; Posner, 1957).[1] The Peruvian upwelling is linked to the persistence of the south-east trade winds, which, when coupled with the rotation of the earth, tend to drive the surface water away from the coast (e.g., Wyrtki et al., 1976; O'Brien et al., 1981). The colder, nutrient-rich, deep water then upwells to the surface where photosynthesis can occur. Although the Peruvian upwelling is considered to be relatively persistent, variability within the system does take place. The Peruvian upwelling has been well researched by the scientific community in the past (e.g., CUEA, JOINT II, etc.) and continues to receive widespread interest by researchers in the oceanographic and atmospheric sciences (e.g., Tropical Oceanographic-Atmospheric Newsletters).

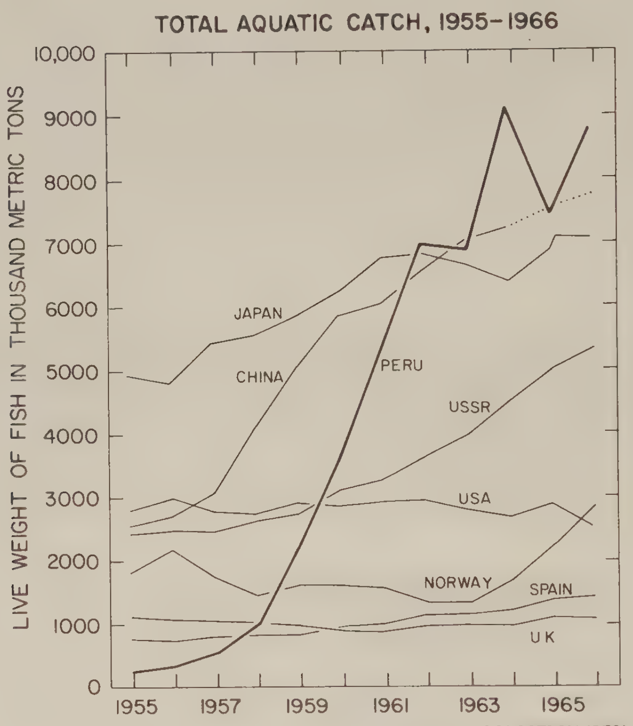
---

[1] Coastal upwelling is the process whereby relatively persistent winds drive the surface water away from the coast, allowing deeper, nutrient-laden colder water to take its place. When this upwelled deep, nutrient-rich water enters the sunlit (euphotic) zone, photosynthesis takes place and the nutrients are then consumed by microorganisms and predators at higher trophic levels. Five major coastal upwelling zones (those centering on Peru, California, Mauritania, Somalia and Namibia) that make up only 0.1% of the ocean's surface supply 44-50% of all commercial fish landings (Intergovernmental Oceanographic Commission, 1974).



There are also several less productive or more seasonal (as opposed to persistent) coastal upwelling systems, such as the Malibar and Orissa coasts of India, Ghana, Java, and Costa Rica (Cushing, 1975).

The Peruvian coastal upwelling region was found to be abundant in anchoveta which had great potential value as a commercial fishery. With an increase in world demand for fishmeal following World War II and with the collapse of the Californian Pacific sardine fishery in the early 1950's, U.S. interest in fisheries shifted to Peru (Boerema and Gulland, 1973). Factories for fishmeal production were built in Peru in the early 1950's, discreetly at first, so as to avoid making suspicious the politically powerful guano industry[2/] which sought to block large-scale exploitation of the fish on which the guano birds depended (Paulik, 1971). The guano industry's blocking efforts in the 1950's and 1960's failed (Boerema and Gulland, 1973). From the mid 1950's to the mid 1960's the Peruvian anchoveta fishery underwent what might be called meteoric growth, as can be seen from the following fish landings statistics (Figure 1).



(SOURCE: BORGSTROM 1972)

By the end of the 1960's, when the fishmeal industry had developed into one of the most productive in the world and when a relatively large number of people had become involved in or affected by it, there were greater possibilities of social dislocation resulting from a major oceanographic-meteorological event known as El Niño than had been the case during the early stages of the development of the Peruvian fishing industry.

Coastal upwelling, El Niño, and the Peruvian fishery

El Niño is generally defined as the invasion of warm water from time to time into the upwelling region of the eastern equatorial Pacific that adversely affects primary productivity and thus the standing stock of anchoveta. While there is no widely accepted definition of El Niño, it becomes clear from a collection of definitions from various sources that there is a sometimes explicit, sometimes implicit, social component to many of the El Niño definitions. For example, some have viewed any invasion of warm water that does not affect the established economy of the region (in the Peruvian case, the anchoveta fishery) as a non-El Niño event. What might be considered an El Niño by Ecuadorian observers might not be considered one by Peruvians. Indeed, one Ecuadorian

---

[2/] Guano is the excrement of anchoveta-consuming birds (cormorant, gannet, pelican, etc.) that inhabit the rocky barren islands along the Peruvian coast. It is a fertilizer that has been mined commercially since the 1840's and sold as an export as well as used within Peru (see for example, Levin, 1960; Miller *et al.*, 1974).

observer noted that his country was constantly faced with El Niño conditions. Furthermore, what might be considered an El Niño by scientists might not be considered one by fishermen. Thus, in addition to the scientific definitions of El Niño, from a societal standpoint it can be viewed as an occasional invasion of warm water into the eastern equatorial Pacific that has a harmful effect on the established economy of the region.

El Niño events have occurred 'quasi-periodically' in past centuries (Murphy, 1926; Ramage, 1975). According to Ramage, there have been at least eight major El Niño events in Peruvian waters between 1900 and 1975, events which he defined as having encompassed two summers and one winter (in the southern hemisphere). Every El Niño event varies in intensity, duration, and magnitude and thus its ecological and societal impacts also vary (Paulik, 1971). Wooster and Guillen (1974) have distinguished the major El Niño events from the minor ones. Recent ones have occurred in the 1957-1958, 1965-1966, and 1972-1973 (see, for example, Bjerknes, 1966; Paulik, 1971; Miller and Laurs, 1975), and had major socioeconomic and environmental (and sometimes political) implications for Peru, as was the case in 1972-1973 (Caviedes, 1975; Miller and Laurs, 1975; Wooster and Guillen, 1974). 1976 was yet another El Niño year, but apparently not a major one by the geophysical definition.

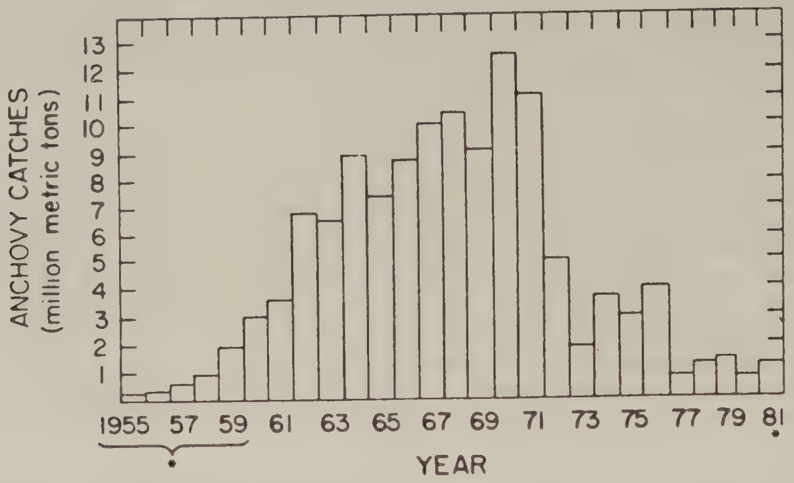
This year scientists have been suggesting that we are witnessing the development of a major El Niño event (U.S. National Weather Service, 1982; Tropical Oceanographic-atmospheric Newsletter, 1983; Philander, 1983). It began in the Southern Hemisphere Fall of 1982 and has continued into 1983. Its unusual characteristics when compared to previous El Niño events, such as its rate, location, and timing of development, may challenge the current definitions and wisdom about such events (Rasmusson and Carpenter 1982; Weare, 1982; Quinn, 1984). Because of its magnitude, its apparent differences with earlier El Niño events, and its hypothesized linkages with seasonal weather in North America and elsewhere (e.g., O'Brien, 1978; National Research Council, 1982), there has been a resurgent interest in this phenomenon by the popular press (e.g., Golden, 1983).

The 1972-1973 El Niño has been blamed for the recent near-collapse of the Peruvian anchoveta fishery and the resultant poor state of the Peruvian economy.[3/] The impact on society of that El Niño was major, because by the late 1960's Peru had become one of the world's largest fishing nations, accounting for 22% by tonnage of the world's commercial landings (Lima Times, 18 March 1977, p. 7), and a major exporter of fishmeal (Glantz, 1979).

In fact, the high level of fishing activity in 1972 obscured the poor state of the stock and the initial effects of El Niño, leading eventually to a sharp decline in the Peruvian catch, in fishmeal exports, and to adverse changes in Peru's balance of payments. Peru's anchoveta catch, on which its economy had to a large extent become dependent for foreign exchange, dropped from an all-time high of 12.4 MMT (officially reported) in 1970 to less than 2 MMT in 1973. In the next three years the anchoveta catch did not go above 4 MMT. In 1977 the fishery was closed in the spring and a ban was placed on fishing anchoveta for the rest of the year.

3/ El Niño was not the only climate-related anomaly to occur in 1972, but was one of a set of events that had a deleterious effect on the global food production system as well as on the perceptions about the system's ability to feed its members (Garcia, 1981). The USSR, for example, registered one of its worst shortfalls in grain production as a result of drought (Katz, 1973), and resorted to major grain imports from the USA (Trager, 1975); this in turn contributed to a scarcity of wheat on the world market. That year droughts also occurred in Central America, the Sahelian zone of West Africa, India, the People's Republic of China, and in parts of Australia and Kenya (FAO, 1974). As a result of the 1972 anomalies, along with other socioeconomic factors (such as the impacts of, as well as reactions to, those anomalies), global per capita food production and global food reserves declined for the first time in more than twenty years (Brown, 1974). In addition to these events and the decline in Peruvian fish landings, there was a simultaneous decline in fish landings in other regions, challenging the assumption that the oceans would be a source of food that could supplement agricultural production to feed the growing populations of the world (see, for example, Thompson, 1977).

Since 1977 the anchoveta catch has not surpassed the 2 MMT level (Figure 2).



• Estimated

In May 1973, the Peruvian government nationalized the fishing industry - fleet and plant capacity - ostensibly to establish a degree of economic rationalization within the industry and to preserve their anchoveta fishery. The nationalization led to discontent and unrest. Fishermen and many of the entrepreneurs felt that they would have had a better chance on their own ('survival of the fittest'). Others, however, heavily in debt, favoured nationalization, which saved them from bankruptcy. Fishermen were subsidized by the government and told when and how much to fish, until the fleet was denationalized in mid-1976. The decision to denationalize the fleet was a result of the poor state of the Peruvian economy, which at that time was plagued by major financial crisis, and, in particular, by the high cost to the government of subsidizing fishermen and the fishing fleet during years of poor catches. The denationalization led to political unrest among fishermen and factory workers. Many of those who had fought against nationalization now fought against denationalization, because they knew that catches would be low due to the poor state of the standing stock.

As a result of the sharp decline in the productivity of the Peruvian fishery in the early 1970's and a decline in the production of anchoveta fishmeal since 1972, alternative sources of livestock feed (such as soybean) began to compete successfully with Peruvian fishmeal (Kolhonen, 1974). Thus, the fishery is of less importance on a global scale, relatively speaking, today than it was a decade ago.

This brief introduction to the Peruvian situation sets the stage for the sections that follow, using the three levels of analysis. The international level is discussed first, primarily because it provides the broadest context for fisheries management. In addition, it is at that level that the attentive public comes into contact with fisheries, when the popular press describes such newsworthy events as the "cod war" between Great Britain and Iceland, the "lobster war" between France and Brazil, international conflicts related to the 200-mile jurisdiction, the impact of factory ship on marine resources, the potential for harvesting krill in the Antarctic, and the seizure of tuna boats in coastal waters of western South American countries.

THE INTERNATIONAL LEVEL

> In other Latin American countries, many development planners are asking how Peru created a first-class modern industry so quickly on such an unprecedented scale. Is there a lesson here, I asked, for other nations?
> (Stroetzel, "Fishing for meal," 1965)

Few commercial fisheries can be considered truly national. Even when the international community is not directly involved in a national fishery, the fishery will surely be affected by factors that originate in other nations.

Such factors can affect the supply of fish and might include, for example, the transfer of technology (including technical advisers), jurisdiction over coastal waters, the need for foreign exchange, and loans from international development agencies. They can also affect the demand for fish products, and might include such factors as international market demands, competition from other fisheries, and international commodity prices for fish products. A third set of international factors might encompass aspects that do not appear to relate directly to fisheries management, and could include, for example, reactions of the international community to the expropriation of foreign investment in sectors other than fishing or to the seizure of foreign fishing vessels.

Underlying these international considerations one finds differing, often opposing, ideological perspectives about society through which each of these actions is filtered. While those with differing ideological perspectives may agree, for example, that a specific activity transpired, they often disagree about its causes or its consequences. Ideological considerations affecting the Peruvian anchoveta fishery will be discussed in the section on the individual level of analysis.

Territorial waters

Many coastal countries whose living marine resources are or have been exploited at high levels have blamed long-distance trawlers and factory ships from other countries for the apparent depletion of their resources (see, for example, Gulland, 1979; Kaczynski, 1979). Factory ships can process, prepare, and store fish catches for several weeks before they return to port. They are accompanied by a fleet of vessels that deliver their catches to the mother ship. These ships have generally abided by international law, operating outside the territorial waters of coastal nations. They operated as early as the 1920's (off the coast of California), but more extensively on a worldwide scale between the 1950's, and mid 1970's. Often local fishermen of coastal states would deliver their catches to these ships rather than to factories along their own coast because of higher prices for their catches.

Countries that have relied on the use of factory ships, such as the USSR, South Korea, Poland, and Japan, could send them to a fishery, and efficiently capture and process their catches without having to limit their operations to coastal areas where port or processing facilities existed. Referring to the northwest African situation, as an example, Crutchfield and Lawson (1974, p. 14) have noted that:

> Before 1969 only two fishmeal factory ships in the world exploited pelagic stocks. In 1970 at least six such ships operated off northwest Africa...(Each factory ship) has a daily processing capacity of 1,000 to 3,000 metric tons of fish, which are provided by ten to twenty modern purse seiners. Storage facilities on a factory ship allow it to carry enough raw material for a day or two of processing and to accumulate meal and oil for several weeks without unloading.

Representatives of many coastal nations have voiced their concern that factory ships and long distance trawlers would deplete their coastal living marine resources, long before they could develop a national fishing industry. Crutchfield and Lawson (1974, p. 14), reinforcing that concern, suggested an hypothetical example of how devastating the fish harvesting technology of those ships could be: "a fleet of ten factory ships could harvest and process...the 1969 Peruvian anchoveta catch (9 million metric tons) in ten months."

Factory ships involved in fish reduction have been implicated in the past in the demise of some important pelagic fisheries, such as the Californian Pacific sardine fishery as early as the 1920's (e.g., Ahlstrom and Radovich, 1970; Radovich, 1981) and the pilchard fishery off the coast of South West Africa (Lees, 1969). They have also been blamed for the depletion of stocks in many other parts of the world, including the highly productive waters off the northwest coast of Africa (e.g. Crutchfield and Lawson, 1974) as well as in the North Atlantic. Thus, factory ships as well as long-distance trawlers presented a clear danger to the survival of coastal living marine resources in various regions around the world until the mid 1970's. Their sphere of operations, however, has been greatly curtailed with the recent adoption by many coastal states of the 200-mile extended economic zone. As noted in the FAO EEZ Programme (1981b, p. 3),

> The opportunities for coastal communities to manage their fisheries were greatly restricted when many, if not most, commercial stocks lay both within and beyond the limits of a narrow territorial sea. Now these countries have a chance to use the fish resources in ways that will benefit their peoples and economies as well as enable them to conserve a renewable resource.

In 1947, Peru protected itself (inadvertently) from this important international aspect of fisheries exploitation that was yet to become popular, by barring foreign factory ships from their waters. In that year, Peru claimed 200-mile territorial waters. The 200-mile claim was rejected by the United States because, at that time, most states, including the United States, claimed a 3-mile territorial limit and a 12-mile fishing limit. According to some observers, an additional factor reinforcing the U.S. reluctance to accept the claim by Peru and other South American states to the 200-mile limit was that it was developing a tuna fishery and the pursuit of tuna would require American vessels, among those of other countries, to go within 200 miles of the coasts of Peru and Ecuador.

There have been frequent international incidents when these South American governments, regardless of the ideological perspectives of the government in power at the time, authorized their navies to capture those vessels that violated their territorial waters. The fishing companies (or their flag countries) were then forced to pay large fines. For example, one celebrated case in the 1950's pitted Aristotle Onassis against the Peruvian government, which demanded the payment of a $3,000,000 fine in return for the release of his whaling vessel that had been fishing in its waters (U.S. News and World Report, 17 June 1955, p. 87). With respect to the U.S. violations, Goodsell (1974) summarized this situation, noting that

> ...more than 35 interceptions of U.S. boats were made between 1953 and 1970. The offenders are escorted to the nearest Peruvian port where they are required to pay fines and penalties amounting to as much as $15,000 per boat (p. 132)....After very few seizures in 1970-1972, during which time schools of tuna failed to appear off Peru, at-sea captures became common once again in 1973 (p. 134).

Ironically (to some observers), these South American governments apparently got the idea for extending their territorial waters from a policy statement by U.S. President Truman, who declared the continental shelf off the U.S. coast to belong to the United States. According to Wesley Marx (1967, pp. 202-3),

> When President Truman annexed the seabed of the adjacent continental shelf, Chile, Ecuador, and Peru looked at theirs. Citing the Truman Proclamation as a precedent, they extended their borders to possess sole sovereignty and jurisdiction... not less than 200 miles from the coast.

Outside the territorial waters, which until the mid 1970's were still generally taken to be up to 12 miles (with the notable exceptions of Peru, Ecuador, and Chile), the living marine resources were considered a common property resource and therefore beyond the jurisdiction of any single nation. Garrett Hardin (1968) popularized the concept of common property resources when he wrote about the "tragedy of the commons." In his popularization which, of course, had been preceded by other papers on "the fishery commons" (e.g., Gordon, 1954), Hardin discussed how a resource (the preservation or protection of which was the responsibility of no one authority) could be misused to the point of destruction. His original discussion related directly to rangelands and livestock, but many authors have since applied the concept of the tragedy of the commons to other common property resources (e.g., Hardin and Baden, 1977). Because Peru's coastal marine resources had been excluded from international exploitation, its yet-to-be-developed anchoveta fishery was spared from becoming another overexploited international common property resource. Thus, by declaring a 200-mile limit, some of the major, often troublesome, international aspects of fisheries management were avoided by Peru during the development of its anchoveta fishery.

The other side of this coin, however, was that Peruvian governments have (collectively) had to bear responsibility for the successes and failures of the management of their anchoveta fishery. When the near-collapse came in the early 1970's, Peruvian leaders could blame neither foreign factory ships nor neighbouring countries for the overexploitation of their main stock of anchoveta off the central coastal area. They could only blame nature and, more specifically, El Niño events (Tantalēan, 1978, p. 250) as the primary cause of the reduced productivity of their anchoveta fishery.

Influence of other fisheries

Another major international aspect of the development of the Peruvian fisheries concerns the origin of its fishmeal industry, and has to do with a different fishery thousands of miles from Peru, along the west coast of North America.

The Californian Pacific sardine fishery had flourished for decades since the early 1900's and was at its peak in the 1930's (see, for a pictorial history, Reinstedt, 1978). By the mid 1940's, it became apparent to all but the wishful thinkers that the continued productivity of that fishery was in question (e.g., Radovich, 1981). Its apparent decline was manifested in the quantity and quality, as well as the southward shift in location, of commercial landings. Despite a brief increase in recruitment in the late 1940's, the fishery had essentially collapsed as a viable economic activity by 1952.

As a result of the impending collapse, California fishing industries were plagued with idle fleet and fish processing capacity, with no fish to catch or to process. This situation was graphically portrayed by the American novelist John Steinbeck in his books Cannery Row and Sweet Thursday. With respect to the idle fleet, one observer noted that

> Some vessels apparently were diverted to other fisheries, others were sold out of the state or the country, still others were scrapped....Some sardine vessels were diverted to the U.S. tuna fishery...and others were sold to Mexico where the sardine fishery off the Baja California was still good (Ahlstrom, quoted in Diegues, 1983, pp. 20-22).

The underlying conditions for the development of a food and/or industrial fishery in Peru had already been established in the early 1940's, when, for example, foreign assessments of biological productivity in Peruvian waters proved to be extremely favourable (e.g., Horna, 1968, p. 394; Roemer, 1970, p. 46). Another underlying international condition for any possible development of such a fishery was the rapidly increasing international demand for fishmeal as a feed supplement for poultry and livestock in the post World War II period. Caravedo (1977), among others (e.g., Culley, 1971), suggested that the catalyst for development of the Peruvian anchoveta fishery came when the owners of the idle fishing vessels and fish processing plants in California decided to sell that capacity to Peruvian entrepreneurs, enticing them with extremely advantageous financial arrangements (see also Horna, 1968, p. 397).

Some American companies joined with Peruvians to establish cooperative arrangements and subsidiaries to exploit the anchoveta for reduction to fishmeal. In an historical account of the first fifty years of the American company that built the first commercial fishmeal factory in Peru, (Wilbur-Ellis, 1972) it was noted that

> ...the ultimate success of Wilbur-Ellis in Peru is largely traced to a meeting in San Francisco between Brayton Wilbur and Manuel Elguera. Elguera was a Peruvian businessman deeply interested in developing his nation's fishery....It was through this close friendship that Wilbur came to participate in the...establishment of the most flourishing fishery in history (p. 14).

Idle Californian fleet and plant capacity was also sold to South African entrepreneurs in the early 1950's, providing an impetus to the development of that fishery as well as that of Peru (e.g., Diegues, 1983; Marx, 1981; Lees, 1969; Culley, 1971). In fact Culley (1971, p. 211) has even suggested that the South and South West African fisheries might have expanded more rapidly than they did in the late 1940's and early 1950's had it not been for the rapid development of the Peruvian fishery in the 1950's. This view has been questioned, however, because South African fisheries began as a food fishery whereas Peru was developing an industrial fishery.

Technology transfer

Another major international aspect of fisheries management in general, and of the Peruvian situation in particular, has been technology transfer (e.g., Diegues, 1983; Gulland, 1972, p. 175; Lees, 1969, p. 201). The implications of technology transfer in the economic development process have been the subject of great interest for the past few decades and have stimulated a great debate on the role of technology in the development process in developing countries (e.g., Goulet, 1977). There have been successes and failures (e.g., Farvar and Milton, 1972). Shärfe (1979, p. 53) has commented that in addition to successes in the realm of fisheries, "unfortunately, there also have been a good number of costly and frustrating failures - mainly due to attempted introduction of overly sophisticated technology combined with a lack of understanding of local cultural, social and economic concerns." Technology, however, can be viewed as neutral. Whether its effects on society are favourable or adverse will depend on how it is used. One author (Goulet, 1977, p. 17) has referred to it as a two-edged sword, suggesting that "although it brings new freedom from old constraints imposed by nature, tradition, or ancient social patterns, technology also introduces new determinisms into the life of its adepts."

There are many examples of new technology being incorporated into the Peruvian fishery. The development of the nylon net has been cited by numerous authors as a major breakthrough for entrepreneurs wanting to invest in fisheries (e.g., Roemer, 1970; Horna, 1968; Lee Smith, private communication, 1983). Nylon nets were more expensive than the cotton nets they replaced but they were also more durable. Thus, nylon nets lowered the long-term costs of anchoveta fishing. Roemer (1970, p. 47) noted that

> Technological progress probably played a key role (in the fishmeal boom). In particular, in 1956 nylon nets began to replace the easily broken cotton ones, and the cost reduction was sufficient by itself to make the industry profitable in Peru.

It became more attractive for Peruvians to buy into the fishery, especially given the favourable terms that were being offered. In fact, a competition for Peruvian markets began and, as Horna (1968, p. 397) noted,

> By 1955 foreign businessmen and manufacturers began coming to Peru to offer their products. The Japanese offered nylon nets priced up to $12,000 with 18 months to pay. When Norwegians extended their credit to two years, the Japanese lowered their prices and matched the two year credit period. Engine manufacturers engaged in a wild scramble to gain customers.

The use of the nylon net was in itself not bad but restrictions related to increased access to the fishery, resulting from the use of such nets, should have been considered. In other words, an assessment of the implications of nylon nets on the development of the fishery might have identified some of the problems that accompanied the "lower costs" to buy into the fishery by eager Peruvian entrepreneurs.

This particular technological input occurred at a propitious time. The fishmeal entrepreneurs had recently won a major political victory defeating the efforts by the Guano Administration Company and their supporters (and more broadly the agro-exporters) to block the development of the fishmeal industry. The victory was due in part to the fact that the prices of guano and agricultural commodities had fallen and, independent of that, there was an increase in price and demand for fishmeal. Reinforcing this point, another observer (Caravedo 1977, p. 110) suggested that in 1954

> The prices of agricultural export products declined in the international market, and production had to be transferred to new export activities that could contribute to an equilibrium in the balance of payments.

Other technological transfers that affected the exploitation of the fishery include the power block, echo sounder, purse seiners, vacuum pumps, and so on. Each new additional input of technology or technique increased the efficiency of fishermen in capturing the anchoveta. Each addition to plant or fleet capacity stimulated a desire, as much as a need, for larger catches, which in turn required greater efficiency in capture and processing techniques.

As mentioned earlier, by the early 1960's the Peruvian anchoveta fishery had become the number one fishery in the world (based on the tonnage). Its fleet, equipment (power blocks, nylon nets, echo sounders, purse seines), and processing capability were quite sophisticated. According to the Encyclopedia of Marine Resources (Firth, 1969, p. 510),

> The Peruvian fishing industry caught 9.76 MMT of anchoveta in 1967, operating a fleet, exclusively devoted to anchoveta, of 1,536 boats of which 58% are steel-hulled ....Of all the boats, 98.5% are provided with echo-sounders and 82.9% with power blocks; only 76.9% of the boats have special pumps to transfer fish from net in the water to the hold.

In addition, the boat owners and their captains and crews were becoming wiser fishermen (e.g., the learning bias factor). With respect to this factor, Gulland (1968, p. 2) noted that

> The influence of the skipper on the catches is a major factor in any fishery.....Up to 1963 the size of the fleet was increasing between 50% and 100% each year. That is, in each year between one-third and one-half of the skippers were fishing for anchoveta for the first time at least as skippers....In 1966/7 the situation was different, in that most of the fishermen had three to five years' experience.

Over time older boats were replaced by newer, bigger, and better equipped vessels. Processing plants were also replaced by newer ones incorporating the most modern technology, much of which had been transferred from such developed fishing nations as Japan, the United States, and Norway.

Included as an element of technology transfer would be technical advice provided by foreign experts. Kasahara (1978, p. 106; see also Shärfe, 1979), commenting on the general problem of technology transfer for fisheries, lamented the fact that

> (Developing countries) are swamped with advice, technical assistance, equipment selling, fishing agreement or joint venture offers, international funding proposals, etc. from various sources. A combination of these usually tends to result in overcapacities by building up a fishing fleet and shore facilities too rapidly since they appear to be cheap and sometimes free. The administrators of at least some of these countries are incapable of sorting out good advice and offers from bad ones.

As with technology, there are successes and failures with technical advice as well (see, for example, Glantz, 1980a). It is important to keep in mind some cautionary concerns that have been raised about the use of foreign experts in fisheries development and management. For example, an expert with the U.N. FAO (Schärfe, 1979, p. 54) suggested that

> Outside consultants often are not well versed in the cultural, social, and economic aspects of the local fishing situation, so they are often unable to offer meaningful solutions to problems. And because the government officer in charge of fishery operations may not have full subject matter competence, there is often a gap in understanding on both sides contributing to an unsuccessful transfer of technology.

Many of these experts provided advice to industry and government on how (as well as why) to develop and expand its fishery, nonetheless. As another example, Diegues (1983) noted that, in addition to boats and processing equipment, the industrialists involved in selling off components of the Californian Pacific sardine fishery also exported to South and South West Africa and to South America valuable expertise that had been accumulated in the California industry. "These exports of capital and know-how, it is often claimed, greatly facilitated the takeoff of the new pilchard and anchovy processing industries of those countries" (p. 22). Finally, an important Peruvian fishmeal manufacturer also referred to the transfer of technical know-how from California to Peru in the early 1950's when he commented that

> It would be unfair of me if I were to omit special recognition for the permanent friendly attitude and the advice and assistance given to the Peruvian fishing enterprise by American institutions and scientists, mainly from the State of California. (Quoted in Marx, 1967, p. 214.)

A different international aspect related to technical advice for the Peruvian anchoveta fishery would be the establishment of an institute for marine research to study the fishery and the biology of the anchoveta. In 1960 the Marine Research Institute of Peru began these studies as a project of the U.N. Special Fund undertaken by the U.N. Food and Agriculture Organization. In 1964 the Institute was renamed the Instituto del Mar del Peru (IMARPE). Later an anchoveta stock assessment was undertaken by foreign and Peruvian scientists (under FAO/IMARPE sponsorship) in order to provide those in government and industry who were involved in managing the fishery with "the first appraisal of the extent of the anchovy stock and of the effects of fishery on this stock" (Boerema et al., 1965, p. 1; see also, Kesteven, 1981).

Almost immediately, IMARPE scientists and foreign consultants began to warn about the increasing possibility of overfishing. For example, as early as this first stock assessment report in 1965 (Boerema et al., 1965, p. 2) they concluded (with some reservations) that

> There is further evidence that a state of the fishery has been reached where additional effort will result only in an insignificant increase of total catch and in further marked declines of catch per unit of effort.... It is thus concluded that the fishery cannot be much further expanded.

For these scientists, the task of aiding in the development of a management strategy calling for the self-restraint of the fishing community or restraints imposed by government agencies on that community was extremely difficult, especially in the absence of reliable and, perhaps more important, visible indicators of depletion of the anchoveta resource. Foreign expert panels were convened on an ad hoc basis beginning in the late 1960's to advise on biological as well as regulatory aspects of fisheries management (e.g., IMARPE panel reports). In 1969, for example, IMARPE convened a panel of foreign economic experts to assess various regulatory schemes for the fishery. That panel concluded (IMARPE 1970) that the fishery was in great danger of collapse because of the excessive pressures on it from overcapitalization of the industry's fleet and plant processing capacity. The report also noted (IMARPE, 1970, pp. 5-6) that

> A substantive reduction in the capacity of vessels and plant... would greatly diminish the grave threat to the anchoveta stock ensuing from the financial difficulties of part of the industry which, particularly when fishmeal prices are high and fish are scarce, lead to strong pressure to relax the necessary catch restrictions.

Nowhere in the report, however, was there any mention of the potential impacts of an El Niño. Thus, the potential combined effect of overcapitalization of the fishing sector and the known variability of the environment were not considered by this panel.

The occurrence of the 1972-1973 El Niño at a time of high fishing pressures and immediately following a 1971 stock recruitment failure sent the Peruvian anchoveta industry into a sharp decline, as reflected in catch statistics for the early 1970's (see Figure 2). In 1976 the IMARPE scientists continued to warn the Fisheries Ministry about the possible adverse effects of reopening the anchoveta fishery prematurely, before the standing stock had a chance to rebuild.

The Minister of Fisheries convened a consultative group of foreign fisheries experts in 1977 apparently to evaluate the conservative advice he had received from the Peruvian scientific community. According to the consultative group's report (Ministry of Fisheries, 1977, p. i), "The group's work consisted of reviewing, testing and challenging the results, interpretations and conclusions, questioning the methods employed, and seeking to assess the accuracy of the results obtained."

The advice of the Peruvian scientists to the Ministry was upheld by these foreign experts (Ministry of Fisheries, 1977, p. 12). That the government had such a meeting at all suggests a lack of confidence by fishery managers in the advice of their Peruvian scientists. (This issue is discussed in more detail in the analysis of the national level.)

Economic development policies

Yet another international aspect of the fisheries relates to Peru's policies toward economic development. Peruvian leaders, especially between 1948 and 1968 and once again after the 1980 election of Belaúde Terry (whose government had been overthrown in 1968 by the military coup of Velasco), have, to varying degrees, favoured a policy of export-led development. This development strategy is based on the export of primary resources (as opposed to manufactured goods) in order to earn foreign exchange which can then be used to finance economic development on a national scale. Peru has often been criticized by Third World development economists as well as marxists because of its pursuit of economic development through exports.[4]

Export-led development can be categorized as a national level factor (to be discussed in the following section), if one assumes that the initiative for its pursuit has been national as opposed to having been imposed by other countries. This development strategy, however, does have important international aspects. For example, fishmeal exports are affected by foreign currency exchange rates (see for example: Brown, 1965; Kuczynski, 1977). Kuczynski, a high ranking government official in the 1960's (and again after 1980), has discussed the impacts on the Peruvian fishing industry of variations in prices for fishmeal in the international marketplace. Fishmeal exports are also affected by the

---

4/ With respect to dependence on exports, Peruvian leaders have been criticized for their pursuit of policies favouring export-led development. Dependence on the revenue derived from primary exports has been cited as fostering colonialism, neo-imperalism, and underdevelopment. Many instances are cited to show that development in an export sector has little impact on other areas of society. These have been referred to as export enclaves (Miller *et al.*, 1974). However, unlike many developing countries whose economies are based on the export of only a few primary products, Peru has a diversified export-based economy that in theory should buffer it from the fluctuations at a given time of price and demand in the international marketplace of any single export commodity.

availability of similar or substitutable exports from other countries with which they compete for markets. Kuczynski (1977) recorded his belief that fisheries provided an unstable base on which to build a development programme, because of the highly variable nature of resource availability.

One of the major competitors to fishmeal is soymeal, and the relative prices of these competing products can also affect the activities in the Peruvian fishing community (e.g., Vondruska, 1981). In fact, the near collapse of the Peruvian anchoveta fishery in 1972-1973 stimulated the sharp increase in price for fishmeal which became an additional consideration that encouraged other countries, such as the United States and Brazil, to devote more of their agricultural lands to soybean production in order to get a greater share of the livestock feed market.

An optimistic assessment (World Fishing, February 1978, p. 31) about the role of fishmeal in the development process has suggested that

> In developing countries there are good reasons why a particular fish resource may not be utilized as a source of food....It is much more feasible to consider the establishment of fishmeal industry which will provide a basic earning power by the export of the product.

Yet, recent projections about fishmeal have presented a more pessimistic view (Robinson, 1982, p. 7):

> The fishmeal market seems to have suffered permanent damage because of the shortages and very high prices which followed the collapse of the Peruvian anchoveta. Compounders are now less keen to include fishmeal in their feeds, although they would if price and advantages became marked.

As a final comment, it is important to note that some actions that seemingly affect only one sector of the economy might be shown, upon closer scrutiny, to have international impacts on other, unrelated, economic and social sectors. The Peruvian dispute with the American-owned International Petroleum Company (IPC) illustrates this point (see, for example, Kuczynski, 1977; Goodsell, 1974; Olson, 1975). Lingering uncertainty that surrounded the outcome of a Peruvian dispute with the IPC apparently reduced the flow of U.S. development assistance to Peru in this period. Largely as a result of the Peruvian desire to take control of its natural resources (a national level action), and doubts about an outcome favourable to American interests, the per capita U.S. A.I.D. capital assistance and grants to Peru had been among the lowest in Latin America for the 1963 to 1968 period (Kuczynski, 1977, p. 125). According to Kuczynski, President Belaũnde believed that

> The financial problems of his regime would be alleviated if AID could lend Peru the same amounts it made available to Chile or Colombia. Instead of relying on expensive supplier's credits, loans from the IDB (Inter-American Development Bank) and from AID would now become plentiful (p. 260).... President Belaũnde had been right in seeing that some agreement with IPC would unlock the foreign aid dam (p. 262).

An agreement was finally reached in mid 1968 between the Belaũnde regime and the IPC, only to be annulled a few months later, following a military coup that established General Velasco's leftist regime (see also Goodsell, 1974). By 1969 all IPC assets in Peru had been seized by Velasco and a multiyear dispute ensued between Peru and the United States about what would constitute "swift and just" compensation for the expropriation. This takeover, coupled with "continued seizure of American tuna clippers inside the 200-mile limit and the establishment, for the first time by a Peruvian government, of diplomatic ties with communist countries drove the U.S.-Peruvian relations to the lowest point in a century" (Goodsell, 1974, p. 84). A Peruvian commented in an interview that "the IPC problem has created a big international question mark which has effectively shut off foreign credits and foreign investments" (quoted in Goodsell, 1974, p. 84).

Against the backdrop of this takeover and the announced intentions to nationalize communications networks (newspapers, radio, etc.) and to implement radical agrarian reform, "Rumors began to circulate (about six months after the coup) that the fishmeal and mining industries would also be expropriated" (Goodsell, 1974, p. 84). The fear of government takeover of the fishing sector surely had some effect on fisheries management.

Summary - International Level

An important aim of this section has been to dispel a belief that what happens in one fishery is of little consequence, except in the marketing sector, to other fisheries in other regions exploiting similar but independent stocks. The Peruvian situation suggested that the rapid development of its fishing industry was precipitated by the collapse of the Californian Pacific sardine fishery. Apparently, that collapse was also a major factor in the development of the South African pilchard fishery.

Today we see a repetition of that experience, only the roles of the actors have changed. Peru, for example, has been attempting to sell its surplus catch and processing capacity in the international community. Fishing News International (October 1981) noted that "Surplus plants are to be offered abroad to the best bidders, although Pescaperu officials also talked of possible joint ventures with international companies." (Pescaperu is the government company set up in 1973 to run the nationalized fishmeal industry.) The same issue of Fishing News International noted that Pepesca ("the money-losing Paita canning and freezing plant") was trying to find a buyer for its tuna fleet and that Mexico, in the midst of large-scale development of its fisheries, has shown interest in this sale.

As another example, South African fishing companies have shown great interest in Chile's pilchard stocks,[5] following the collapse of the South West African pilchard fishery in the late 1970's. Fishing News International (April 1981, p. 9) reported that

> A joint venture between a Chilean group and two South African fishing companies is to set up two new factories in the northern ports of Iquique and Caldera....Much of their machinery is coming from Walvis Bay where factories of the South African companies had to close due to the depletion of pilchard stocks.

Thus, it becomes quite clear that there are many linkages between the national development of a fishery and the international community concerning when, how, why, and by whom the coastal living marine resources of a country are exploited and managed.

5/ During the mid 1960's, when the Peruvian fishery was at its peak, Peru was engaged in exporting boats and plants to Chile (Stroetzel, 1965, p. 19). There are several interesting accounts about how the Chilean fishery was developed in its northern-most province and what the role of the Peruvian anchoveta fishery was in that development (e.g., Caviedes, 1981; Salinas M., 1973).

THE NATIONAL LEVEL

> When the war came to Monterey (California) and to Cannery Row everybody fought it more or less, in one way or another. When hostilities ceased everyone had his wounds. The canneries themselves fought the war by getting limits taken off fish and catching them all. It was done for patriotic reasons, but that didn't bring the fish back.
> (Steinbeck, Sweet Thursday, 1954)
>
> While catches decline and policy conflicts escalate, national fishing strategies can continue to vacillate between costly subsidies, technical fixes and wishful projections.
> (W. Marx, The Oceans: Our Last Resource, 1981)

The second level of analysis focuses on aspects of the national political process and on those groups that might impinge on the way in which the coastal living marine resources are managed. There are many events that take place in a given country that are national level activities which might directly or indirectly affect the management of marine resources; for example, the issuance of government decrees related to agrarian reform as well as to fisheries, worker strikes in the mining sector as well as in the fisheries, policies toward exchange rates (encouraging or discouraging exports and/or foreign investment), government nationalization of foreign investment in, for example, extractive industries (oil, copper, iron) as well as in the fishing sector. The fishing sector is only one subsystem embedded in a larger political system. In order to understand how the fishery is managed, it is necessary to be aware of that broader context.

In addition, there are political pressures with which leaders must constantly cope, such as the fear of a military coup or the lack of support of the press, political groups, or the legislature (e.g., Kuczyinski, 1977). These activities, many of which are not obviously related to fishery management, consume the attention of political leaders, and take time from other pressing issues, including the oversight of the management of the nation's coastal fishery.6/

To present all such events for Peru (or, for that matter, for any other country) would be to reproduce its history, which is not the purpose of this section. This section will focus on (a) how conflicting objectives (goals, aims) for fishery management pursued by various groups in society might affect resource management and (b) political changes at the national level and their implications for fisheries management. There are other potentially relevant second-level actions that, at first glance, might appear to be unrelated to fisheries but in fact have proven to have major implications for the fishing sector. One such example might be the Peruvian expropriation of the International Petroleum Company (IPC) in 1969, which was an act based on political and economic nationalism at the national level. However, at the international level it served to heighten the reluctance of the U.S. government and, for a while, of the international development banks to provide development loans to Peru, until that issue was resolved to their satisfaction. This state of affairs adversely affected the general financial situation in Peru, making it all the more difficult for the government to continue its support for the nationalized fishery. Investigations of these less obvious factors are worthy of additional research.

6/ For example, one of the major socioeconomic problems in Peru in the 20th Century has related to land reform. The large land owners in control of the most favourable agricultural lands have been challenged by peasants with little or no land favourable for agriculture. Each government has felt the political pressure for land reform. This has been a major preoccupation of most postwar governments in Peru. Harding (1975, p. 229) for example, suggested that "By the time political parties were functioning again leading up to the 1956 elections, they were all promising agrarian reform."

Objectives in conflict

As noted in the international section, instead of becoming an international common property resource, the Peruvian anchoveta fishery became a common property resource at the national level. Of course, the end result of unregulated exploitation of a common property resource is often the same: over-exploitation and a high risk of depletion. An FAO pamphlet on the State of the World Fisheries reinforced the view that the attitudes that lead individuals, groups, or nations to over-exploit a fishery classified as an international common property resource exist for national common property resources as well (FAO, 1981b; see also Robinson, 1980).

> Even where stocks have been exploited by one nation alone, the common property aspect has still had a damaging influence. Unlimited access to fish stocks and the competitive features of multinational fisheries, have been duplicated within national fisheries.

Clark (1973) raised an additional concern when he suggested that it might even be in the interest of a corporation (regardless of whether it is national or multinational) to exploit a fish stock to extinction (see also Gould, 1972). Hammergren (1983, private communication) has speculated that in the Peruvian case, the anchoveta was seen more as a means by which to achieve land-based development goals than as a development goal itself (despite Fisheries Minister Tantalean's attempt to raise the national consciousness about Peru's marine resources). Such an attitude could lead (unwittingly) to the severe depletion of the fish resource. The validity of such arguments (which, in theory, seem plausible) would show that how a fishery is exploited is more related to the objectives of the exploiters than to the number of international or national actors involved in that exploitation.

Each group in society pursues its own goals. These goals or objectives often conflict. As Gulland (1974) has suggested, "everybody concerned with fishing will have slightly different ideas on what the proper objective of fishery management should be." Yet this phrase, "slightly different ideas," is a rather mild description of competing interests pursued by groups locked in a struggle for a share of a finite fish resource.

The fact that these are competing interests (i.e., objectives) can adversely affect the management and viability of a living marine resource in which these groups have an economic, social, or political stake. Gulland also referred to "the proper objective." This phrase, too, can be misleading, as it suggests that there is one true objective reality to which all might agree. One must keep in mind the assertion presented in a recent ACMRR Working Party Report on Management (FAO, 1979a, p. 7) that "What is important is the clear recognition that there are different classes of objectives - biological, economic, and social - as well as different time horizons over which objectives might be obtained."

One can find objectives stated by different groups involved in the exploitation of the same resource that are diametrically opposed to each other. While John Gulland's statement appears to belabor the obvious, it apparently requires constant reiteration. As the ACMRR Report (FAO, 1979a,p. 7) suggested, "There is an infinite range of biological, social, economic, and political objectives determined by local circumstances. Each of these objectives, if followed, could lead to a different pattern of harvest and exploitation."

Every observer acknowledges that it was in the interest of the Peruvian Guano Administration Company, for example, to minimize the exploitation of anchoveta for reduction to fishmeal. While it was in the interest of the Guano Administration Company to block the development of an industrial fishery based on the exploitation of anchoveta, it was in the financial interests of Peruvian investors (from all walks of life) to invest in the capture and processing aspects of the anchoveta fishery. While it has been perceived by entrepreneurs to be in the interest of the fishmeal manufacturers to process as much fish as possible to increase production efficiency and for the boat owners to capture as many fish as they could to increase their profits and to pay off their loans, it is the objective, at least in theory, of fishery managers to assure through regulation that the resource will be available for future generations. Marine scientists may favour a more conservative approach to anchoveta exploitation because of the many uncertainties in the marine and atmospheric environments.

Bankers may wish to encourage development of a certain sector and make loans available to willing entrepreneurs. On this, one author (Stroetzel, 1965, pp. 20-21) suggested that after the mid 1950's (the beginning of the fishmeal boom) engine manufacturers were saying "put down 25 per cent cash on a diesel and we'll finance your boat" (see also, Horna, 1968, p. 398). Bankers were reported as telling potential investors "Put up a third and we'll lend you the rest to build a processing plant." As an example, those in the banking sector may wish to stimulate growth in the fishing sector by making loans available to potential investors at favourable rates, so that there will be spillover of economic activity into other sectors to support the fishing sector, such as boat, net and gear manufacturing, that would develop in support of the fishing sector. The bankers may achieve their objective but, as a Panel of Experts Report (IMARPE, 1970, p. 376) noted,

> Surplus processing capacity encourages plant owners to expand their fleets in order to obtain larger shares of the allowable catch, thereby permitting them to improve profitability through wider spread of plant overhead and fixed costs that higher plant utilization bring with it.

Thus, such expansion in capacity will in turn lead to additional pressures on the fish resource. Objectives pursued by these groups often conflict with each other, and the attainment of some objectives (goals, aims) precludes the attainment of others.

Different approaches to economic development can lead to different objectives in the exploitation of living marine resources. If, for example, a government's objective is to improve the nutritional intake of its people, it may favour the development of a food fish industry either to increase domestic consumption of protein-rich products directly; or, in a country where fish is not a major source of protein for its people, a government must decide between making fish products acceptable to consumers within its country or selling those products in the international marketplace, and then using the foreign exchange to upgrade the population's nutritional intake (e.g., investment in those sectors of society that supply the people with their traditional protein needs).

On the other hand, the government may decide to forego the development of a food fishery in favour of a reduction fishery. This has been viewed as an unholy choice by some observers. In 1927, for example, during a legal conflict between Californian sardine canning and reduction interests, one observer commented that "It seems repugnant to every right-thinking citizen to see fresh fish used for any purpose other than human consumption" (Ahlstrom and Radovich, 1970, p. 186). This concern about the conflict between food and industrial catches extends into the present. For example, Popiel and Sosinski (1973, p. 228) have addressed this issue, noting that "Rapidly expanding industrial catches along with steadily increasing fishmeal production in the last decades have been watched with anxiety by countries whose fishing fleets operate mainly for fish for human consumption." Most recently, Mexico's Department of Fisheries decreed that its "sardine and anchovy industries must place the feeding of people before the feeding of animals" (Fishing News International, September 1981).

Fishing industries have developed worldwide based on the production of fishmeal, which can command a high price in the international marketplace under favourable circumstances, and can produce sorely needed foreign exchange. Foreign exchange (in theory) can then be used to finance economic development. Referred to as export-led development, Peru has been no stranger to this approach to economic development (e.g., Levin, 1960; Roemer, 1970; Miller et al., 1974; Kuczynski, 1977).

In addition to problems created by conflicting objectives, problems exist with the interpretation of "wise" or "prudent" management of living marine resources. While every group registers its explicit support for the conservation of the standing stock, their individual as well as their collective behaviour brings to question whether their members want or know how to pursue conservation practices in the face of the highly variable physical and social environments, especially in the absence of objective (as opposed to subjective) guidelines for carrying out conservation strategies. For example, different groups have cited as their strategies competing theories, such as maximum sustainable yield, maximum economic yield, optimum yield, prudent yield, safe yield, and so on (e.g., Clark, 1976; Gulland, 1974). Yet there are many uncertainties that surround the sustainability of a pelagic fishery under fishing pressure. Thus, many of the models used to explain or to estimate "optimal" catch levels are often no more than crude approximations. Garth Murphy (1977) has suggested that for pelagic fisheries, these models have been of little value (due as much to the nature of these fisheries as to problems with model construction). How useful or consoling to fisheries managers in Peru is the following statement (Murphy, 1977, p. 298)?

> As might be expected from the record of steady recruitment, the 1965-1971 fishery appeared stable and well managed, though the industry had clearly overexpanded. By this is meant that simple biomass yield models, such as the logistic and exponential could be fitted, exhibited rather reasonable variance, and all suggested similar maximum sustainable yields of 9.5 - 10.5 million metric tons per annum, a level not far exceeded during any year.

Conflicting interest: Guano versus fishmeal

An example of a conflict between diametrically opposed goals would be instructive. One of the earliest conflicts between objectives that was related to the fishery took place between those seeking to exploit the anchoveta and the Guano Administration Company's representatives[7] who opposed such exploitation. The Guano Administration represented an extractive industry dominated by the traditional elite in Peru. A threat to its interests was seen in any effort to exploit the anchoveta (Murphy, 1954; see also Kesteven, 1981). Despite the fact that the Guano Administration Company was among the first to experiment with exploiting the whole anchoveta for the production of fishmeal (as opposed to fish byproducts from the fish canning operations), it vigorously opposed any new attempts to establish such an industry.

In 1950, however, a whole fish reduction plant was clandestinely established along the Peruvian coast. A few years later, when the market prices for guano and agricultural exports were declining (a quasi-periodic event) and the demand and prices for fishmeal were increasing, President Odria's market-oriented policies gave those interested in developing a fishmeal industry a major boost. Despite repeated attempts throughout the 1950's by the guano "lobby" to restrict the annual landings of anchoveta (e.g., Caravedo p. 110), the fishmeal industry as well as associated industries such as shipbuilding, processing plant construction, net manufacture, gear production, etc., developed rapidly (e.g., Freyre, 1965, p. 406).

The debate between the fishmeal producers and the Guano Administration Company and its agro-exporting supporters centered on the possible combined effect of the exploitation of the anchoveta by both the fishermen and the guano birds. In the absence of scientifically-based stock assessments in the early years of the industry, there was little if any hard evidence on which to oppose the development of a foreign-exchange-producing industrial fishery. Commenting on this, Manuel Eleguera, one of the first Peruvians to

---

7/ Through the mismanagement of the exploitation of the guano resource (the mining of it at rates faster than it could be replenished), the guano industry was clearly on its way to destruction by the end of the 1800's. To bring about a rational exploitation of guano, the Guano Administration Company was established by the government in 1909 in order to oversee the extraction of the guano and the protection of the guano-producing birds (Levin, 1960). For decades the Administration managed the exploitation of guano as well as the protection of the guano-producing birds and the enhancement of their productivity (Murphy and Murphy, 1959). Guano production, however, had declined drastically since the fishmeal boom began, dropping from 330,000 tons in 1956 to 52,000 tons in 1970 (Massey, 1972).

participate in the development of Peru's fishmeal industry, noted (1964, p. 54) that

> In 1955, the government tried to force the fishing industry to restrict its catch to 100,000 tons a year. Even though the catch at that time was about half the suggested quota, the industry strongly opposed the quota system, since there were no studies to justify the measure and because it considered it incompatible with the free enterprise principles applied to all other economic activities in this country.

The government's policies vacillated between supporting the demands of one or the other of the two interest groups until the late 1950's. Smetherman and Smetherman (1972, p. 342) reported that

> In 1956, the guano interests pressed the government into ordering a halt on further construction of fishmeal plants until studies were made of the effect on the bird population. This decree was lifted in 1959, marking a defeat for the guano industry.

Once the influence of the guano and agro-exporting elite had been overshadowed by the influence of the potentially lucrative fishmeal industry, there was little interference by government in the industry's operations until 1968. One of the major Peruvian fishmeal producers commented on the fact that industry determined fishmeal production policy, not government. Eleguera (1964) noted that

> All this impressive industrial complex has been built by the efforts of private enterprise. And even the most important phases of present government and fishing policy are due to initiatives from private enterprise and not to government.

Elguera also suggested that "If we had left it to government, Peru would never be the fishing giant it is today" (Stroetzel, 1965, p. 20).

Government agency objectives

Yet, in spite of industry's dominant role in the growth and development of the fishmeal industry in Peru before 1968, government agencies, too, with their own narrowly defined jurisdictions, pursued different, often conflicting, objectives. By the 1960's, government agencies viewed the fishery as an earner of foreign exchange and as a direct source of government revenue through the implementation of taxation policies for exports and imports. These agencies sought this revenue in order to support development elsewhere (i.e., not in the fishery). This often led to the establishment of regulatory policies that tended to conflict with (and even cancel out) policies pursued by other agencies. Tax credit policies, for example, formulated in the Finance Ministry tended to encourage expansion in fleet and processing capacity which contradicted the policies of those whose objective was the prevention of overfishing by the reduction of overcapacity. As Hammergren (1981, p. 327) has noted, "Even when the government gave tax or credit relief, it tended to encourage further investments in the already overextended industry and to help some marginal operators to hold on longer." Thus, if one group benefits from an expansion of processing facilities, that benefit may adversely affect other groups and the resource as well. "Surplus processing capacity encourages plant owners to expand their fleets in order to obtain larger shares of the allowable catch," as the IMARPE Panel of Experts (1970, p. 376) noted, "thereby permitting them to improve profitability through wider spread of plant overhead and fixed costs that higher plant utilization brings with it."

There have been several government agencies, as well as the Congress, involved in activities related directly or indirectly to the fishery. According to Hammergren (1981, p. 323), "fishing policy was not coordinated by any single office but was shaped by the diverse (and often conflicting) interest of the various agencies involved, agencies for which fishing policy was not a primary concern..."There has been no ultimate arbiter of group conflicts, no coordinator of group objectives, no Super-Ministry of Fisheries. In fact, it was not until 1970 that a separate Ministry of Fisheries was established by President Velasco (this activity had been within the Ministry of Agriculture and its Division of Fishing and Hunting). Not all observers agree, however, that increasingly centralized decisionmaking for the anchoveta fishery is beneficial. For example, in an interview in 1976 (Pesca, June-July 1976, p. 21), the first fishmeal factory owner to have his plant nationalized (in 1973) suggested that

> The greatest error made with the industry is to give to one man - the Minister of Fishery - the control of the scientific information about the presence of the anchoveta, the control of the marketing of fishmeal and his only power to decide the opportunity to go fishing or not.

In part as a result of fragmentation in the government bureaucracy with respect to the fishing sector, and in part as a result of the successes of the industrialists in exploiting the fishery with little visible evidence of damage to the resource, it has been difficult to bring into force any viable, widely acceptable, prudent management scheme for the anchoveta, regardless of the government in power. Gulland (1977, p. 7) has commented on the general nature of this point, noting that "In the past the cry 'do not decide yet, the evidence is not really conclusive' has prevented timely conservation and management of resources threatened with overexploitation."

Following the first scientific assessment of the state of the anchoveta stock in 1965, there have been annual responses by fishery managers to the advice of IMARPE's marine scientists. These responses (i.e., fishing regulations) have been controversial with respect to their effectiveness as administrative measures to protect the resource (e.g., Valdez-Zamudio, 1973).

Scientific uncertainty and conflicting objectives

A major problem for decisionmakers directly or indirectly responsible for fisheries management is scientific uncertainty. There is enough uncertainty in scientific information about living marine resources that whatever the recommendations of the scientists, even foreign scientific advisers, the validity of their recommendations could be questioned by the entrepreneurs, fishery managers, and high ranking government officials. As Pedro-Pablo Kuczynski (1977, pp. 140-41), an adviser to President Balaũnde, noted

> A problem that exists in the relationship between tẽcnico and politicians is the degree to which they trust each other. The politician tends not to believe gloomy predictions by the tẽcnico, who therefore feels he will not be listened to unless he exaggerates....It was only natural for the Executive (in this case, Belaũnde) to be more inclined to listen to rosier predictions.

Such a lack of confidence has hindered the development of trust and credibility between scientist, fishery manager, and policymaker. The general lack of confidence among these groups existed in the 1960's (Kuczynski, 1977) and in the early 1970's as well (Tantalean, 1980), making it somewhat easier for the policymaker to give in to the pressure of the moment (political, economic or other) rather than to act in accordance with the scientific advice. Tantaleãn Vanini, Fisheries Minister under Peru's President Velasco, commented on how he viewed the role of IMARPE scientists (Tantaleãn, 1980, p.247):

> IMARPE is an organization to assess and recommend; the final decision of what has to be done has to be with the Chief of the Sector. For example, to determine the opening of the season, its ending, or the closures, first I listened to IMARPE's scientific recommendations, then looked to the needs for foreign exchange, in coordination with the Ministry of Economy and Finance, and coordinated with EPCHAP, which was in charge of commercialization (of fishmeal), read the reports of the boat owners, analyzed the

> social factors and observed the activities of our neighbours. Naturally, the recommendations of IMARPE should be followed but it should not be thought that the boat owners could not make good recommendations.

As another example, as late as the beginning of 1972, the marine scientists at IMARPE advised the government about the weak anchoveta recruitment of 1971, but politics or wishful thinking appears to have overridden their scientific advice. As Clark (1977, p. 61) has written,

> The event of 1971-72 provides a case in point. By March 1972, when the fishery reopened after a 2-month summer closure, it was apparent to the IMARPE that there would be little recruitment. The Instituto recommended that the fishery remain closed to conserve the spawning stock, but the government allowed that fishery to operate until June, by which time the stock was reduced to a very low level. It seems from this record that the adult stock was simply fished out.

Conflicts between scientific advisers and government representatives appeared again in the mid 1970's. By the time of the occurrence of the 1976 El Niño, the fishery had not returned to what fishermen, among others, considered to be the "normal" conditions of the 1960's, that is, to the level of catches witnessed during its heyday just six years earlier. Peruvian scientists were calling for an embargo on anchoveta fishing for a few years in order to allow the standing stock to rebuild. At that time the government was in deep financial crisis and, as some suggest, on the edge of bankruptcy. It could not afford to continue support for the fishing sector. Yet the government had nationalized the fishing sector, including the fleet, three years earlier and was subsidizing the fishermen during a period when there was little fishing activity. As mentioned earlier, the Fisheries Minister convened a confidential panel of foreign marine resource experts to assess the advice (and the scientific information on which it was based) of his fisheries advisers. The panel's findings upheld those of the Peruvian scientists (Ministry of Fishery, 1977, p. 12). Fishing activities for anchoveta off the central coast of Peru were greatly curtailed. In this instance government officials heeded, apparently reluctantly, the advice of national and foreign advisers. In many instances, however, such has not been the case. Addressing this general problem, Gulland (1977, p. 8) has warned that "Attempts to reassess the scientific evidence for the sake of administrative convenience are unlikely to be to the benefit of science or (except in the very short run) of administration."

If one wishes to avoid identifying the differing objectives of all groups related to the fisheries, one might separate those groups that seek to conserve the resource from those that seek to derive an immediate benefit from its exploitation, with little "objective" regard to conservation. The aim of the former group could generally be represented by a statement from the IMARPE (1970) report that placed conservation before immediate profit by noting that "The first objective of any system of regulation and management of the anchoveta fishery must be to ensure the continuation of the substantial contribution to the Peruvian economy."

The goals of the latter group have generally centered on the economic value derived from exploiting the anchoveta fishery either directly by fishing or processing the fish; or indirectly by building fishing vessels or supplying them with needed gear such as floats, nets, engines, etc.; or very indirectly by reaping the support of a constituency favouring policies that might adversely affect the fishery. Industrialists, for example, may feel pressured to increase the level of exploitation of a fishery in order to reduce immediate monetary (economic) hardships (Diegues, pers. comm.), giving little regard to the long-term effects of such an increase. In addition, as investors, they may view the fishery in a different light than do other members of society. Popiel and Sosinski (1973, p. 2258) suggested that in general

> Fisheries for industrial purposes do not show as much concern for maintaining stocks of fish as fisheries for food. This comes from a greater flexibility of the former, which having overfished one species can easily shift to another, since the kind of fish exploited is of little importance. (emphasis mine)

Finally, not all interests in a society have the same political leverage and some interests apparently dominate the political process at a given time. For example, in Peru, the influence of the agro-export and guano interests dominated that of the anchoveta fishmeal interests only to have their positions later reversed. The influence of the fishmeal interests dominated that of the food fish industry only to have their positions recently reversed. Gulland (1977, p. vii) has suggested that

> In practice management policies will have to be determined in each case in the light of current objectives of society (whoever determines what those might be), and of the scientific understanding of the stocks, bearing in mind that they will never be completely accurate. (emphasis mine)

It is important, therefore, to identify the dominant and subordinate interests in a society for an improved understanding of how a fishery has been or might be managed.

Changes in national government

Brian Rothschild (1973, p. 2022) suggested that "The emphasis based on various objectives is not the same in different political systems; different desires (may exists) for foreign exchange, for 'status' in fisheries, and for maintaining options for the future..." The same can be said for changes within political systems as well. 8/

Political authorities at the national level are often the source of broad policy guidelines that establish ground rules by which various economic sectors in society, including fisheries, might operate. To date, there have been a dozen changes of government in Peru since 1939, as shown in the following table.

8/ Political systems, according to David Easton (1965), can be divided analytically into three components: political authorities, regime, and political community. Political authorities are those in positions of power with day to day responsibilities of government. Regime represents the authoritative rules and structures that provide order to the political interactions within a political system. The political community has been defined as "a group of persons bound together in a political division of labor" and can exist in a tribe, a nation, or a state.

A change of political authorities within a political system (in this case, Peru) can be frequent. While there can be considerable continuity from the policies pursued by one set of authorities to those pursued by another, there can also be considerable change. Not all changes in political authorities will lead to a change in regime, however. In the Peruvian situation, there was a relatively high degree of continuity in development strategies between 1948 and 1968, despite the changes in national leaders. However, changes in political leaders in the 1945 election and the 1968 coup did lead to attempts to change the regime.

Rulers of Peru

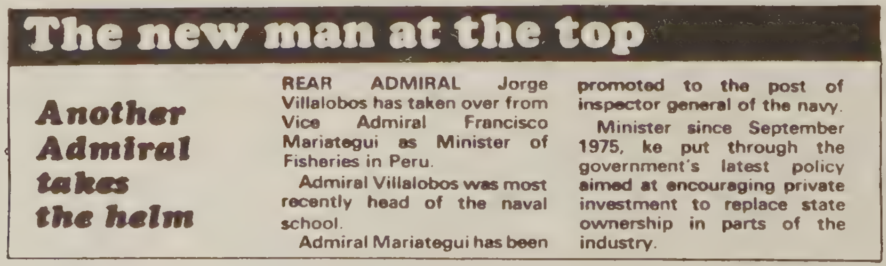
1939 to 1945	Manuel Prado y Ugarteche
1945 (July) to 1948 (October)	Jose Luis Bustamante y Rivero
1948 (November) to 1950 (June)	Manuel A. Odria Amoretti
1950 (June) to 1950 (July)	Zenon Noriega
1950 (July) to 1956 (July)	Manuel A. Odria Amoretti
1956 (July) to 1962 (July)	Manuel Prado y Ugarteche
1962 (July) to 1963 (March)	Ricardo Perez Godoy
1963 (March) to 1963 (July)	Nicholas Lindlay Lopez
1963 (July) to 1968 (October)	Fernando Belaunde Terry
1968 (October) to 1975 (August)	Juan Velasco Alvarado
1975 (August) to 1980 (July)	Francisco Morales Bermudez
1980 (July) to present	Fernando Belaünde Terry

On some of these occasions new Peruvian governments pursued policies that were major (if not drastic) changes from those of their predecessors, especially in 1948, 1968, 1975 and 1980. Each new set of government leaders brings with it its own political, economic, and social programs, and personnel. Often this calls for changing the national priorities that their predecessors have placed on particular economic activities. For example, one government may be more concerned with agrarian reform, another with oil extraction, yet another with the mining sector. The political importance of ministries (and their ministers) rises and falls because of changes in government or because of changes within a government. For example, Kuczynski (1977, pp. 27-28, 76) noted that "expenditures and tax administration fluctuated with the coming and going of each minister. During the Belaũnde administration (1963-68) there were altogether seven holders of the (Minister of Finance) portfolio in slightly more than five years (four in the last year alone)."

Changes in government can also directly affect the leadership of various functional agencies throughout government and, depending on the degree of government involvement in society, throughout the social system as well. More specifically, change in high ranking personnel in ministeries related to the management of fisheries (e.g., the Ministry of Finance) is an important consideration for why the same resources may have been managed in different ways. Kuczynski (1977, p. 77) commented on the linkages between opposing international perspectives toward development and opposing domestic perspectives, noting that

> The early 1960's were the heyday of the conflict between the so-called "ECLA" (U.N. Economic Commission on Latin America) and "IMF" views, and the conflict between (Peru's) Planning Office and the Central Bank tended to mirror the international institutional difference....The prevalence of one point of view or the other certainly made a practical difference in fiscal policy.

To many scholars interested in universal problems, what might appear as a relatively unimportant news item, such as the change of personnel in a government agency, may ultimately prove to have had a profound effect on how a resource has been managed. For example, such a change in personnel was reported in Peru in 1979 (Fishing News International, February 1979, p. 82):



The new man at the top

Another Admiral takes the helm

REAR ADMIRAL Jorge Villalobos has taken over from Vice Admiral Francisco Mariategui as Minister of Fisheries in Peru.

Admiral Villalobos was most recently head of the naval school.

Admiral Mariategui has been promoted to the post of inspector general of the navy.

Minister since September 1975, he put through the government's latest policy aimed at encouraging private investment to replace state ownership in parts of the industry.

This relatively unspectacular event did lead to other, more severe changes that were reported the following month (Latin American Economic Report, 23 May 1979, p. 93):

> The new (fisheries) minister has already been shaking up the management of the industry. He has replaced the official in charge of setting the catch...by (someone) who was head of processing under the previous minister. (The new minister) is also reported to have changed the directors of all four fishing zones.

How changes in national government come about may also be an important consideration for resource management (e.g., free elections or military coups). Changes in government bring changes in priorities of specific government programs and can change the ideological foundation for government programs as well. For example, the pretext for military involvement in what might be called a civilian political process often stems from fundamental disagreements between military and civilian leaders concerning the goals of government as well as the means used to attain them. Thus, military rule imposed now and again on society can mean radical changes from previous government policies. In addition, there are sure to be major changes in government personnel as military men are placed in key positions throughout the economy. Thus, large swings in the ideological directions of governments and their economic development programs are to be expected.

The military can also influence the operations of government and can intercede in the political process, if its leaders oppose a policy direction that the elected leaders favour. This was the case in Peru in 1962, when it opposed the results of a civilian election. In that instance, the military leaders chose to rule for only one year. In fact, a threat of possible military intervention in the political process may be sufficient to change the behaviour and the policies of a government.

Peruvian Governments, 1939 - Present

The first Prado government was established in 1939 at the outset of World War II. Prado implemented temporary controls on exports, with the reluctant and ambivalent support of the Peruvian export community. Perhaps the wartime situation, and the belief that the control measures were temporary, allowed the affected communities to accept such restrictions. Their expectations proved to be no more than wishful thinking because, as Brown (1965, p. 107) noted,

> What they could not realize was that when the time came for dismantling the controls, Manuel Prado's term would be over and the new president would not only be of different inclination and orientation, but in a political situation where economic policy could not be easily formulated.

In 1945 Bustamante was elected president as a compromise political candidate by a coalition of leftists and conservative supporters. Once elected, Bustamante apparently pursued policies independent of those favoured by his supporters. As a result, his regime (1945-48) was plagued by internal political dissension between conservative and leftist elements that all but paralyzed the economy (e.g., Brown, 1965). The government's economic policies were concerned with "inflation, deficit spending, exchange controls and devaluation," and created a relatively undesirable investment atmosphere for American and other investors (Hunt, 1975, p. 303). According to another author (Roemer, 1970, p. 40),

> From 1945 to 1948, the Peruvian government operated exchange controls and kept the sol overvalued in an attempt to transfer income from exporters, who were considered to be congruent with the wealthy class, to those who would benefit from cheaper imports.

Bustamante's attempt at a "controlled economy" was ended by a military takeover of government led by General Manuel Odria. Odria's regimes (1948-50 and 1950-56) developed conservative economic policies that opened up the Peruvian economy to direct foreign investment and to the pursuit of market-oriented policies. Odria favoured a policy of export-led development, relying on the export of traditional primary resources such as guano, copper, silver, zinc, cotton, coffee, and sugar. Unlike other developing countries that exported only a few primary resources, Kyczynski (1977, p. 5) noted that "the growth of exports took place on a broad front, so that Peru acquired a diversified export base."

Odria's changes in economic policies came at what, in retrospect, seems to have been an opportune moment nationally as well as internationally; the California sardine fishery was on the edge of collapse, there was an increase in demand for fishmeal as a poultry and livestock feed supplement, and there were favourable assessments by foreign scientists of the biological productivity of Peruvian waters. The conditions within Peru for investment in fishing were ripe as well, as Horna (1968, p. 394), among others has noted; "Peru had native capitalists willing to risk money investing in the development of a fish industry." He commented that, since 1952,

> when the public became aware of the handsome profits to be gained in the fish industry, everyone wanted to enter the business. Lawyers, dentists, doctors, engineers, teachers, professors and students formed partnerships to purchase plants and boats. (p. 397)

Another researcher commented on the implications of Odria's policies for the nascent fishing sector (Caravedo, 1977, p. 110):

> Since fishing was primarily an export industry, it benefited from Odria's economic policies....This increase was not in response to North American marketing mechanisms as had been the case with the increase that occurred during World War II, but a response to world demand and internal economic policies within Peru.

Thus, the takeover by the conservative military government of Odria in 1948 set the stage for the eventual development of the anchoveta fishery.

Odria's regime was replaced in 1956 with the election of Manual Prado, Peru's president during World War II. The policies of his business-oriented, conservative government concerning foreign investment and export-led development were similar to those pursued by Odria. According to one author (Brown, 1965, pp. 28-30), the following developments within Peru stimulated the growth of the fishmeal industry by the late 1950's: (1) the nylon net, which reduced operating costs for fishing, (2) no noticeable decline in the guano bird population attributable to new fishing factories and (3) the passing of the Industrial Promotion Law, which removed obstacles to the expansion of any industry. To this one could add that a new class of Peruvian nationals was eager to invest in potentially lucrative export schemes (Horna, 1968).

Belaũnde Terry's (1963-1968) government policies were in many ways a continuation of the export-led growth supported by his predecessors (Kyczynski, 1977, p. 48). With respect to the anchoveta fishery, Belaũnde's policy has been described as "one of laissez-faire economics, providing support to the private sector, allowing it to make most of its own decisions." As noted earlier, the administration apparently questioned the scientific advice of its tecnicos, generally considering them to represent a relatively conservative point of view, especially when the government was more interested in "rosier" projections. In addition to this, the government had its own beliefs about where the hope for the future development of Peru rested. For example, Kuczynski (1977, p. 9) noted that

> At the time of the Belaũnde administration, the mining companies held the key to Peru's future prosperity. Mining offered the only opportunity for substantial growth in exports. The other export sectors, such as fishmeal and high grade long staple cotton, appeared to have limited possibilities because production depends on natural supply in the first case or on the availability of irrigated coastal land in the latter.

Belaũnde's government was overthrown in October 1968 by a coup that established military rule under General Velasco. The Velasco regime was ideologically opposed to the economic policies that had been pursued by all of the Peruvian governments since the 1948

Odria coup. The 1968 coup brought to power a leftist military group bent on taking control of the economy away from the established elites. As Jaquette (1975, p. 433) noted, "the Revolutionary Government has made a determined effort to destroy the old power structure rather than accomodate itself to the existing elites."

The new leftist regime claimed that it was "neither capitalist nor communist" and called for a high degree of government involvement in various sectors of the Peruvian economy and society. Its policies were geared toward direct government control of the vital sectors of the economy through nationalization of oil extraction and of mining ventures, of the fishing sector, of the country's news media, and so forth. It fostered citizen participation in land reform programs and established worker participation in management and ownership of many industrial activities, including the fishing sector (Whyte and Alberti, 1977). Hunt (1975, p. 310), commenting on this change in policy, noted that

> From the moment that the armed forces took power in October 1968 and declared Peru to be entered into a revolutionary process, official pronouncements on questions of economic development changed significantly in both language and substance....The change in Peru was particularly abrupt and drastic.

Hammergren considered the 1968 coup a turning point with respect to government interest in the fishing sector "with greater emphasis on centralized planning and government control of the economy" (1981, p. 320). It was as drastic a change with respect to economic policies as was the Odria coup in 1948. Hammergren (1981, p. 317) also noted, however, that "greater government involvement in this sector did not resolve some of the problems of coordination in that sector nor did it lead to less fragmented and less contradictory individual policy decisions."

In 1970, Velasco appointed General Tantaleān as head of the newly established Ministry of Fisheries, a position he held until 1975. The new government sharply reduced the influence of the National Society of Fisheries. It was well known that this society was extremely influential in the formulation of policies that related to the fishing sector. With the 1968 coup, however, the fisheries society had "almost no influence" among the generals (Goodsell, 1974, pp. 86-89). Hammergren (1981, p. 336) supported this contention, noting that "...because of the government's ideological orientation, the sensitivity of the policymaking system had been lessened to former economic elites like the fishmeal producers in particular." Still, during the Vesasco regime, expropriation of foreign investments and socialist property ownership programs tended to dominate the Fisheries Ministry's attention. Hammergren (1981, p. 333) commented on one of the effects of the establishment of the new ministry on resource management:

> From the Ministry's side several factors encouraged a larger catch. One was the inexperience of the new administrators and the inevitable disorganization following the creation of the new Ministry which meant that the catch was not closely monitored and that decision-makers were less sensitive than they would be later to the problems of resource conservation. ....A second factor encouraging large catches was the desire of the new Fisheries Ministry and its Minister to demonstrate their competence.

In 1975 General Morales Bermudez deposed the ailing General Velasco and took over the government. In many respects this military coup (at first viewed as no more than a "palace coup") was as important for the future of the fishing sector as was the 1968 coup. The takeover represented a victory for the conservative elements in the military over the radical supporters of Velasco. The economy of the country was in poor condition as a result of declining prices for export products and of the financial demands of the development policies pursued by Velasco. Morales' policies were geared to reducing government involvement in many sectors of the economy and society, as witnessed by the denationalization of the fishing fleet in 1976. After a new fisheries minister had been appointed in 1979, it was reported (Latin American Economic Report, 23 March 1979, p. 93) that "it remains to be seen whether, like his predecessor, he will put state assets up for sale to the private sector, or whether he will follow a line closer to that of General Javier Tantaleān Vanini, who greatly expanded state control of the fishing industry." In addition, Morales allowed for the preparation and convening of free elections in Peru in 1980. This election returned to power President Belaūnde, who had been ousted in 1968.

The problems associated with changes in government continue for the Peruvian fishing sector (Fishing News International, November 1981):

> Pescaperu...lost part of the market when an inexperienced marketing team came in with the new government last year (1980). 'They broke contact with socialist countries, which were big buyers'....There is a new team now with revised approaches. But they have to recover lost ground.

In the relatively short period of time that the fishing industry underwent very rapid growth (1952 to 1970), Peruvian governments and their policies (and ideological underpinnings) changed frequently, making difficult the formulation, let alone enforcement, of long-term acceptable, "wise" management strategies for the coastal fisheries. These changes in government proceeded in parallel with the optimism of the industrialists about the future availability of the anchoveta resource, encouraging different groups in society to seek the best deal possible for their own interests. It is not difficult to see how changes in government at the national level can affect approaches to economic development which, in turn, can affect for better or for worse the management of Peru's coastal resources.

Summary - National Level

One of the main points of this section is that in addition to the conventional reference to conflicts between major groups, i.e., fishing community, government officials, and fishery managers, there are conflicting views (and therefore conflicting objectives) within these groups as well. Attention has been focused on a factor that affects fisheries management at the national level - changes in political authorities. This is an aspect that is seldom addressed at meetings on fisheries management, because in many countries there is a separation of science and politics. The marine science community is often unable to openly challenge policy decisions once they are taken.

Scientists provide one piece of information to policy makers who then must weight that information with other places that have been provided, for example, by the Central Bank, or by industry. Thus, fishery managers might find that they must go against the recommendations of their scientists in order to meet some other pressing need. As an example of this, Fishing News International (February 1981) reported that "the (private) canners...are competing with Pescaperu, the state fishmeal production and marketing company, which estimates it needs a catch of 1.8 million tons just to cover costs." But what is needed is not an "either-or" decision with respect to societal objectives and scientific information. What is needed is a greater degree of sensitivity by fisheries managers and scientists to the concern of the other. Perhaps the following statement (FAO, Redefining Fisheries Management, 1981b) underscores the need for this heightened sensitivity:

> When biological objectives reigned supreme, the administrator did little more than reject or rubber stamp the recommendations made by scientists. With objectives that are wider and less easily defined quantitatively, the importance of the decision-maker increases. It becomes the fishery manager's job to work toward socioeconomic goals that may well conflict with objectives that might be selected on purely technical grounds where political conflict or social costs would not be major consideration.

INDIVIDUAL LEVEL OF ANALYSIS - HUMAN NATURE AND BEHAVIOUR

> The question for policy is often not "What is reality?"
> but rather, "Whose reality will prevail?"
> (Padelford and Lincoln, Dynamics of International
> Politics, 1962)

Objective assessments of events that take place around us are extremely important. However, different observers have different, often conflicting, perceptions of those events and those perceptions become their reality. It is extremely important to identify those perceptions because they serve as the basis for human actions. While they may not prove to be accurate reflections of reality, the actions taken based on them will be real, as will be the consequences of those actions. Therefore, perceptions are an important element of the individual level of analysis. Three important considerations that relate to fisheries management at this level are as follows: (a) one's view of society's relationship to nature, (b) one's view of the renewability of living marine resources, and (c) ideological perspectives.

(a) Man-Nature Relationship

There are conflicting views about what the relationship between man and nature should be. These views, seldom made explicit, can in fact be spread across a continuum, with one extreme represented by the domination of nature by man and the other extreme represented by man's subordination to nature. Two major views relevant for this paper emerge: man-over-nature and man-in-harmony-with-nature (Kluckhohm and Strodtbeck, 1959).

A central theme of the man-over-nature view is that nature is (or should be) subordinate to mankind. Nature is to be exploited by man (e.g., Spring and Spring, 1974). While there are obstacles that nature places in the path of the human activities, it is man's obligation to devise ways to surmount those obstacles. One way to do this is through a reliance on technology. Goulet (1977, p. 19) commented on cultural values associated with western technology, noting that "By definition technology is interested in getting things done; consequently, it breeds impatience with contemplation or harmony with nature." In many instances the application of technology to resolve one problem has led to other unintended problems (e.g., Borgstrom, 1972). Supporters of man-over-nature contend that the environment is robust and therefore resilient in the face of those "insults." In other words, nature can absorb most, if not all, of the adverse impacts of human activities.

This belief exists in the world of fisheries and tends to foster the development and application of new technologies for the purpose of exploiting living marine resources. For example, the replacement of cotton nets with nylon ones, the use of purse seiners, power blocks, vacuum pumps, echo sounders, and so forth have all been developed to increase fish landings. Each in its own way, these technological fixes enable the fishermen to outmaneuver fish, which, of course, do not have the capability to outmaneuver these new technological applications. Apparently, shoaling by forage fish reduces the effectiveness of natural predators but has served to make such catch techniques as the purse-seine more efficient. "With these techniques," noted Murphy (1977, p. 285), "man has so greatly nullified any advantage of shoaling with respect to protection from predation that these species are readily rendered extinct or near extinct by fishing." Thus, the indiscriminate use of technology in a fishery can adversely affect the long-term productivity of that fishery, bringing it not only to the point of financial bankruptcy for industrial firms but can even bring the fish population to the point of extinction.

The man-in-harmony-with-nature perspective suggests that man must place limits on his capabilities when dealing with the natural environment. It is based on the belief that there are limits to exploitation of the natural environment. Unless those limits are acknowledged and then taken into account in the exploitation of nature, overexploited resources will disappear. Farmers, for example, realize the need for soil conservation practices in order to maintain the productivity of their soils. Foresters, too, realize that rates of exploitation must be in balance with rates of replacement. This view demands that those involved in the exploitation of living marine resources recognize, as well as respect, the limits that the natural environment places on their activities. Supporters of this view of the man-nature relationship also tend to believe in the application of appropriate, as opposed to high, technology. While they do not know with certainty what those limits of exploitation are, they tend to support a conservative level of resource exploitation, favouring, for example, such fishery management guidelines as safe yields (building in considerations of uncertainty) as opposed to optimum economic yield or maximum sustainable yield, which are based on theoretical calculations (e.g., Clark, 1976; Edwards and Hennemuth, 1975).

Believers in either of the two contending views tend to strongly oppose the other view. The man-over-nature group has been pejoratively referred to as cornucopians and optimists, while the man-in-harmony-with-nature group has been called doomsayers and pessimists. While the latter group may assert that "technology is the answer," the former group might respond with "technology may be the answer but what was the question"?

Beliefs held by the various individuals or groups of individuals in a society are not equally influential in the policymaking process at any given point in time. It can be argued that the perceptions that political authorities have about the relationship of man to nature constitute the dominant ideological perspective in the political system at a given point in time. Beliefs held by others can be viewed as subordinate perspectives. Changes in national government or changes by national leaders of administrative personnel in relevant government agencies can bring about a change in the dominant perspective.

Most leaders in developed as well as in developing countries tend to pursue policies of development that are manifestations of the man-over-nature view; that is, relying on human ingenuity to surmount obstacles or constraints laid down by nature. A major difference between the responses by political authorities in developed and developing states is that the former is often in a position to commit greater financial resources either to reverse or at least to mitigate the environmental damage that might result from a disregard for the natural environment.

The Peruvian Experience

The history of Peru has been one of rapid, almost sequential, development of several of its natural resources. As one Peruvian scholar-statesman observed (Kuczynski, 1977, p. 5)

> As in many of the poorer countries, the growth of foreign trade was in spurts, depending upon the exploitation of some new natural resource in high demand. Such was the case of guano...in the mid-nineteenth century; of the development of lead, zinc, copper, and silver mining in the twenties; of the rapid expansion of cotton and sugar products after the Second World War, and of the fishmeal boom in the early sixties.

As discussed earlier, one of the most notable resources related to the Peruvian anchoveta fishery has been guano. Seeking to protect the resource on which the bird population fed, the Guano Administration Company was able for some time to thwart attempts to establish a fishery based on the anchoveta. The beginning of the end of dominance by guano interests over fishmeal interests came with the clandestine construction of the first fishmeal operation in Peru in 1950 (Wilbur-Ellis, 1972). Fearing a rapid growth of the fishmeal industry, the Guano Administration Company hired an American scientist to assess the potential impact of a commercial anchoveta fishery on the guano birds. In the resulting report, Murphy (1954, pp. 213-14) pointed to his (and apparently the Guano Administration Company's) view of the man-nature relationship, when he commented on the wanton exploitation of guano in the 1800's.

> If the heedless human animal could act so adversely upon the world of life, including his own interests, it was equally possible that by using his brains he might be able to create a profitable harmony with nature.

On the interaction that would come about as a result of the proposed development of a major fishmeal production capability, Murphy exposed his belief when he subtitled a section of his report "Man, the Only Insatiable Predator," and wrote that

> It is obvious that natural predators, such as fish, or birds or beasts, can never seriously reduce the number of their prey, because their very existence is determined by the abundance, including a dynamic surplus, of the food organisms. Predator and prey are in equilibrium. Man, on the other hand, is capable of depleting any readily attacked natural resource. Unlike a guano bird, man has no automatic checks and balances upon his operations. He is not directly dependent upon the tissues of his prey for the energy with which he executes his exploitation. A guanay must eat anchovetas in order to catch more anchovetas, but fishermen hunt with energy from a totally different source, such as petroleum. Only the slow and disastrous consequences of exhaustion and financial failure can end their campaign (pp. 226-27).

Those favouring the development of a Peruvian anchoveta fishery outmaneuvered the guano exporters in the political process. The anchoveta fishery was among the latest resource to be exploited by Peruvians and, as was suggested (Smetherman and Smetherman, 1972) at the beginning of the 1970's,

> The Peruvian anchoveta fishmeal boom, unlike earlier Peruvian economic activities such as guano, sugar, copper, silver, and cotton production, would not be another of these boom to bust ventures. (emphasis mine)

There is still controversy over why this fishery nearly collapsed in the early 1970's, with one group blaming the environment (e.g., El Niño), another group blaming poorly regulated fishing activities, and a third group blaming the simultaneous occurrence of both of those events. As time passes, it seems that the El Niño event takes on an increasing share of the blame for the demise of the Peruvian anchoveta fishery.

In the search for socio-economic (aside from geophysical) reasons for the demise, attention often turns to technology. Information about the fish catching and fish processing capacity, cited with pride by representatives of the fishing sector, now became suspect as having contributed to the demise of the fishery. The IMARPE (1970) report, for example, discussed the problem of overcapacity in Peru's fishmeal processing capability as well as in the fleet. It has been reported that during the 1972-1973 El Niño, anchoveta were being captured at rates that far exceeded the ability of scientists to assess those catches. By the time assessments were made and it had been determined with confidence that the fishermen had been cutting into the standing stock, impairing its ability to regenerate its population, the damage to the fishery had already occurred (e.g., FAO, 1979a, p. 108; Troadec et al., 1981, p. 19).

(b) Renewability

Researchers and policymakers have generally accepted the belief that renewable and nonrenewable resources constitute the two basic categories of natural resources. Most observers (optimists and pessimists alike) categorize fish as a renewable resource. This perception of renewability most probably stems from the fact that fish are self-generating, although it is recognized that some seasons are better than others with respect to recruitment.

There are many definitions of renewable and nonrenewable resources. As one example, according to Klee (1980),

> Renewable resources would be those that can maintain themselves or be continuously replenished if managed wisely, such as soils, food crops and domesticated animals, land or open space, water (abiotic), freshwater (biotic), marine, wildlife, or forest resources.

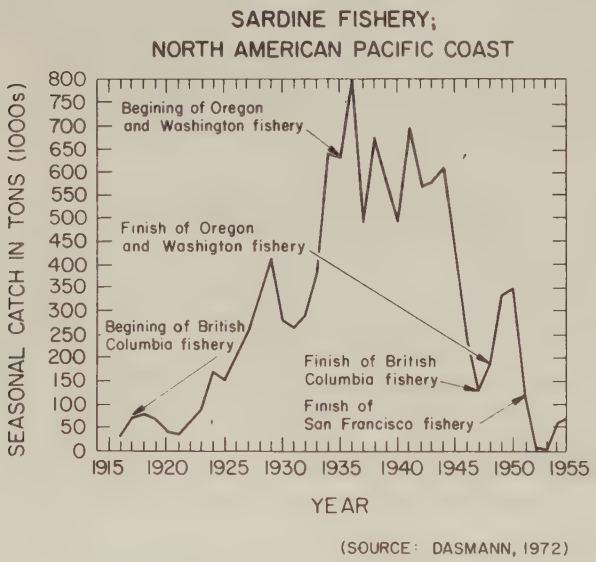
> Nonrenewable resources are those not generated or reformed in nature at rates equivalent to those at which we use them, such as metals, fossil fuels, building materials, fertilizer chemicals, etc.

Pelagic fish resources could conceivably fit into either of these categories, depending on one's assumptions about fisheries. For example, they could be considered renewable with proper management. If exploited at rates faster than they can replenish their populations, however, pelagic fish could also be considered nonrenewable. These definitions suggest that a particular resource in a given place could, over a period of time, move from the renewable to the nonrenewable category, depending on how "wise" the management of the resource might be.

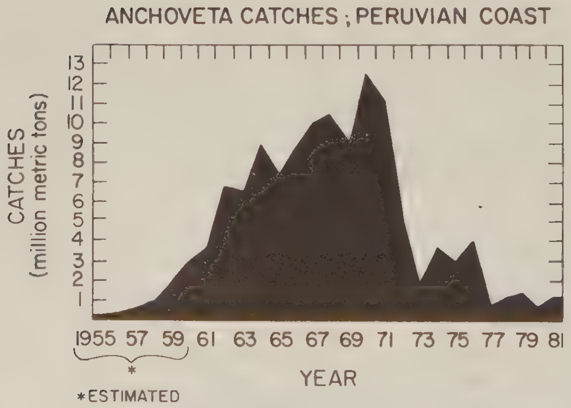
The exploitation of fish populations is surrounded by uncertainties about fish population dynamics as well as about the larger oceanic and atmospheric environments (e.g., a long-term shift in climatic factors). Thus, while fish populations may be viewed as renewable in one context, they may also be viewed as nonrenewable in another.

Pelagic fish can be viewed as depletable in several ways. They can be depleted, for example, to the point of extinction or to the point where they become vulnerable to environmental fluctuation and changes, or to the point where their reduced numbers make them commercially unprofitable to capture. The above discussion is based on the premise that pelagic species are renewable resources, if managed wisely. Are pelagic fish in fact renewable resources and, if so, under what conditions?

The following graphs (Figure 3) show commercial fish landings for three major pelagic fisheries; the Pacific sardine off the coast of California, the pilchard off the coast of Namibia (South West Africa) in the Southeast Atlantic, and the Peruvian anchoveta in the eastern equatorial Pacific.

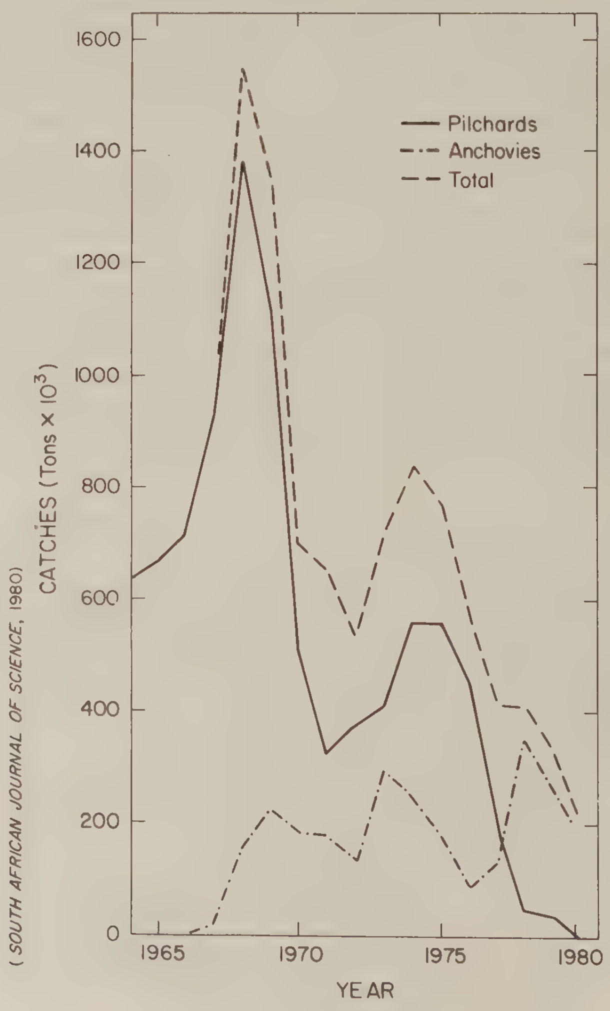

SARDINE FISHERY; NORTH AMERICAN PACIFIC COAST

(SOURCE: DASMANN, 1972)


ANCHOVETA CATCHES; PERUVIAN COAST

(UPDATED FROM GLANTZ AND THOMPSON, 1981)

PELAGIC FISH LANDINGS IN SOUTH WEST AFRICA (1965-1980)



(SOUTH AFRICAN JOURNAL OF SCIENCE, 1980)

As the graphs suggest, each fishery collapsed or nearly did so. For each of these assessments of collapse or near collapse, two opposing schools of thought have emerged about the reason for the demise of these fisheries. Some observers suggest that overfishing was the factor that led to the collapse (each observer may have different views about why the other two fisheries collapsed). In the absence of heavy fishing pressures, they contend, the fish population would probably have been able to cope with fluctuations in its physical environment.

Other observers contend with equal conviction, and often with equally convincing pieces of scientific information, that the collapse of the fish population resulted primarily from changes in environmental variables. While overfishing may have been implicated, the environmental factors set the stage for and were the major cause of the demise. Similar opposing views about the fate of a fishery have not been restricted to these particular fisheries.9/ Garth Murphy (1977, p. 296), for example, noted that

> In Japan (the Far Eastern Sardine) and in California... scientists tended to divide into two camps. Environmentalists maintained that changes in the ocean climate were responsible for the observed qualitative and quantitative changes in the populations. The second camp maintained that fishing was the basic reason for all of the problems. The sardine disappeared.

Assuming that the view that environmental changes brought about a collapse of these fisheries is correct, would it then be valid to assume that fish populations in specific regions can appear and disappear regardless of the intervention of man? If so, might fish populations of a particular kind, in a specific region, and during a specified period of time, be considered nonrenewable resources? Assume, on the other hand, that the view that human intervention (for example, overfishing) was responsible for the collapse of these fisheries is correct. This view calls for "wise" management of pelagic fish resources. Yet the uncertainties surrounding the exploitation of these living marine resources are many, and the task of identifying an acceptable management strategy considered by most observers to be "wise" or safe would be almost impossible. In the absence of regulations that prohibit the exploitation of a particular fish population or of difficult-to-determine prudent management strategies, it seems that most pelagic fish populations that take on a commercial value eventually become severely depleted or collapse altogether.

An added dimension to the consideration of renewability of fish stocks is that the world is divided into nations, each with its own jurisdiction over its coastal resources to the extent of the 200-mile Extended Economic Zone (EEZ). It is, therefore, important and useful to define the renewability of resources at a national, not a global, level. To the country that destroys its forest resources, its coal deposits, or its living marine resources, those resources are gone. Only under extraordinary human effort and cost might they be replaced with similar resources.

Therefore, the concept of renewability should include a spatial dimension (e.g., the Pacific sardine off the coast of California has been "unrenewed"), as well as a temporal dimension (e.g., the resource has not been available in commercially desirable quantities for two decades following its demise in 1952; Williams, 1978). Species can also return after they have disappeared or have been reduced to low numbers in a specific area. For example, there is a debate currently underway about whether the sardine has returned to the coastal waters off California in commercially exploitable numbers (MacCall, 1983). Therefore, it appears that these species can shift from the renewable category for a given period of time to a nonrenewable category at a different period of time. One of the problems for society and the managers of those pelagic fisheries is that they do not know when those species will disappear, become sharply reduced in number, or reappear, regardless of the cause (environmental changes or degrees of overfishing). As Murphy (1977, p. 305) has noted about various kinds of stock-recruitment and productivity models, "even if properly applied (they) are only useful for estimating the average sustainable yield, and hence the size of the industry. They cannot forecast the discontinuous events that have been repeatedly observed, and which often result in population collapse." Perhaps, if under unpredictable adverse conditions they can disappear, pelagic fisheries should be realistically treated as nonrenewable resources.

To the extent that the history of the three pelagic fisheries in separate parts of the ocean, discussed earlier, might serve as examples of exploitation of such resources in other coastal areas, might it not be "wise" to build a consideration of its probable demise into the planning and development of a similar national fishery? If these highly productive fisheries have collapsed, why not expect that others will do the same? If the managers of a new fishery were to accept such a contention (i.e., that a pelagic species that takes on a commercial value tends to collapse), then they may choose to develop the infrastructure to support that fishery at a lower level, knowing that if (or when) the collapse comes, the dislocations it precipitates (e.g., unemployment, loss of foreign exchange, etc.) will be at a much lower level than might have been the case had the resource been treated as renewable.

Renewability and the Peruvian Anchoveta

Those who favoured in the early 1950's the development of a commercial fishery based on Peruvian anchoveta argued that the anchoveta existed in great abundance and for all practical purposes were limitless (e.g., Borgstrom, 1972). At the outset of its development, they argued that an anchoveta fishery would not affect the bird population and guano production; in essence, commercial fisheries and the guano industries could be sustained by the same resource. Robert Cushman Murphy, as noted earlier, cautioned about limits to exploitation of the anchoveta and that in the absence of strict controls on the fishery, the insatiable predator of the two (i.e., man) would destroy both the fishery and the guano industry. In fact, the guano bird population, estimated at more than 30 million before the 1957-1958 El Niño event, had declined to less than two million following the 1972-1973 El Niño and has since returned to more than 5 million (e.g., Tovar, 1983).

Without a scientific basis to decide otherwise, the government policymakers gave in to the fisheries entrepreneurs and allowed the anchoveta to be exploited on a commercial basis as an industrial fish. As more and more people entered the fishery, the catch statistics in the 1950's and the early 1960's suggested that, in fact, perhaps there was room for both the fishermen and the guano-producing birds.

Only when crises appeared (either socio-economic or geophysical), did Peruvians become concerned about the implications of treating the fishery as a limitless resource. In 1965, as a result of a reduced supply of anchoveta and of scientific reports suggesting the fishery was at its limit of exploitation, the government agency responsible for the fishery established its first closed season (veda). By the late 1960's it became abundantly clear that there were too many vessels competing with each other for what all came to realize was a limited resource. It was at this time that the maximum sustainable yield for the anchoveta fishery was calculated to be about 9.5 MMT per year, but that yield included the bird population's consumption of about 2 MMT per year. The irony in this situation was that by the late 1960's the fishmeal entrepreneurs were calling for a planned reduction of the population of anchoveta-consuming birds for the sole purpose of freeing up more anchoveta for their processing plants. For example, Schaefer, a noted marine scientist, addressed this issue in the following way (1967, p. 512):

> Certainly, as a minimum, everyone can agree that it is a priority matter to maintain sufficient populations of each of the bird species to prevent their being driven to extinction, because it is of overriding importance to maintain this genetic material for the future use of humanity. However, one can assert, with some certainty that, for this purpose, there is required a good deal less than 16,000,000 birds.

(See also Stroetzel, 1965, p. 20; and Horna, 1968). This, of course, confirmed Murphy's 1954 assessment of the potential impact of an anchoveta fishery on guano production and his suggestion that "man was an insatiable predator" (p. 226). Murphy had also predicted that the end result of an unregulated anchoveta fishery would be the demise not only of the guano industry but of the anchoveta fishery as well.

Even in the period following the visible signs of overcapitalization of the industry and overexploitation of the resource, those involved with the fishery continued to be optimistic about the future availability of the resource. Much of this optimism appears to have stemmed from wishful thinking, not scientific fact. On this view, Hammergren (1981, p. 345) has commented that

> While government planners were aware of the danger.... Unfortunately, past experience, the demands of an economy in crisis, and the lingering tendency to view resources as inexhaustible in one form or another, do not argue for the more conservative position (of exploitation).

Most recently, a report on the state of the Peruvian economy (Downer, 1980) showed continued signs of optimism about the anchoveta fishery, even after several seasons closed to anchoveta fishing, noting that "Peru's legendary anchovy fishing grounds...are coming to life again after a two-year ban of the fishermen. 'The anchovetas are returning,' said a Peruvian last month, crossing himself for luck." Wishful thinking or unbounded optimism should not be a substitute for objective scientific information.

(c) Ideological perspectives

Opposing ideologies exist and their existence must be accepted even if the contents of that ideology are not. A capitalist, for example, will have a view of the world that differs markedly from that of a marxist. Someone who believes in dependency theory (see, for example, Galtung, 1971) will have a worldview that could differ from either that of the capitalist or the marxist. As Bell (1962, p. 30) pointed out, "The most salient fact about modern life - capitalist and communist - is the ideological commitment to social change."

Ideological perspectives not only might define the causes and consequences of certain actions related to fisheries management or to the management of other economic sectors seemingly unrelated to the fisheries, but might also come into play in the determination of strategies in response to those causes and consequences. It is therefore important analytically to make explicit the ideological worldviews of the various decisionmakers involved directly or indirectly with fisheries, as well as of those observers whose views might be representative of those of various segments of society and who might, through their interpretation of history, influence activities impacting the fishing sector.

At the international level, observers with differing ideological perspectives interpret interactions between states in profoundly different ways. While one observer might note, for example, that foreign investment in a Peruvian fishmeal processing factory was designed to yield profits for both the Peruvian and the foreign entrepreneurs, another observer might view it as exploitation of a developing country by a developed country in order to gain access to its natural resources. For example, an oceanographer (Tomczak, 1981), whose views might be assumed to represent those of a segment of Peruvian society, expressed his belief that

> The economic structure of any nonsocialist country of the Third World is characterized by imperialist control over the larger part of the economy, the largest share of this control being exercized by one of the superpowers, either through direct investment or through foreign debt (p. 403).

According to Tomczak (1981, p. 406), even the changes over time in the relative percentages of Peruvian commodities for export were the result of "a gradual change in the Peruvian economy...as a response to changing imperialist interests."

On the other hand, an executive of the American fishmeal company that constructed the first processing plant in 1950 in Peru asserted that the decision to sell idle California fleet and processing plants to Peruvian entrepreneurs was a decision made as an ad hoc response to the collapse of the Californian Pacific sardine fishery and not the result of a long-range strategy to penetrate the Peruvian economy in general and the fishing sector in particular. At least one of the Peruvian entrepreneurs agreed with that view (Eleguera, 1964).

Ideological interpretations of national level activities related to the fisheries also exist. Consider, for example, conflicting ideological views of the origins of the Peruvian fishmeal industry. In his article on "The State and the Bourgeoisie in the Peruvian Fishmeal Industry," Caravedo, whose views also can be said to represent a segment of Peruvian society, suggested that the growth after 1948 of the fishing industry had been a response within Peru to changes in export policies resulting from a change in economic development programs, following Odria's military coup, and was "not in response to North American marketing mechanisms as had been the case...during World War II" (Caravedo, 1977, p. 110). He also noted that"the initial capital to develop these two sectors of Peru's fishing industry (fishing and shipbuilding) was essentially Peruvian" (p. 105). Caravedo (p. 104) also discussed class struggle and how it affected, as well as was affected by, the exploitation of the anchoveta resource.

> This article shows the form in which industrial fishing emerged, the development of competition between capitals, and the process of monopolization in the sector. Through this process, crisis developed which took the form of the depletion of the major resource - the anchovy. But accumulation in this industry not only led to the depletion of the anchovy, but to the "super-exploitation" of the proletariat.

An opposing view of the Peruvian situation was described by an author (Jaquette, 1975, p. 413), who noted that

> Under military dictator Manuel Odria and elected President Manuel Prado, Peru's economic system has been remarkedly open - that is, market-oriented and hospitable to foreign investment. The maintenance of a free enterprise economy can be attributed in part to the ideological convictions of one individual, newspaper editor and sometime finance minister Pedro Beltran, and to the fact that the open economy favours exporters and foreign investors, two of the most powerful groups in pre-1968 Peru.

As an example of class struggle, Caravedo (1977, p. 104) commented on the implications of the 1973 nationalization of the fishing sector by Velasco's government, noting that "The Peruvian state had taken over the industry in 1973 and compensated many of the capitalist at above the book value of their assets." The nationalization was viewed by him, among others (e.g., Malpica, 1975), as having freed the capitalists from the burdens of a debt-ridden industry that had seemingly lost its resource base, at least temporarily. The buying out of the capitalists, according to these authors, meant they would be free to reinvest in more profitable industries (Caravedo, 1977, p. 120). The actual financial compensation made by government to entrepreneurs has been critically evaluated by Malpica (1975), a representative of the Federation of Fishery Workers, whose criticisms were in turn challenged by Peru's former Minister of Fisheries, General Tantaleān (1978).

Caravedo (1977, p. 104) also attributed class conflict as the motivation behind denationalization of the fleet in 1976, suggesting that

> In 1976 the state declared a state of emergency in the fishing industry, but this time because of the militancy of the working class. After momentarily breaking this militancy, the state returned the fishmeal sector to private hands. The militant workers in the fishing industry who were involved in a strike for job security were massively laid off.

The nationalization, however, was defended by Tantaleān as the only way to bring about economic rationalization of the industry by reducing the existing fleet and processing capacity in order to bring it into balance with the anchoveta resource. To foreign investors, the nationalization by the Velasco government was viewed as the latest attempt to move Peru away from free enterprise and toward communism.

The examples of ideological perspectives, like others in this paper, are illustrative. They were not included to favour one ideological perspective over another but have been presented only to underscore the author's belief that ideological perspectives can affect fishery management.

While some scientists and policymakers may wear their ideological perspectives on their sleeve, so to speak, others may be unaware of how it affects their decisions. As an example of these different levels of awareness of ideology in the Western Hemisphere, Jaquette (1975, p. 402), noted that "The centrality of ideology in Latin American politics (stands) in contrast to the North American experience (where ideological content, although it is possibly just as central, goes unrecognized as such)..."

Summary - Individual Level

The importance of considering aspects of human nature and behaviour must be recognized when considering fishery management. One of the main points in this section is that individual perceptions about abundance and renewability of living marine resources affect how those resources might be exploited. The combinations of these various perceptions about the resource with perceptions about the widespread uncertainties that surround the fishery pave the way for fisheries managers to choose from a wide range of seemingly rational management options.

It is equally important to put the individual in context of the larger social and political organizations in which he operates. However, the tendency to reduce problems of fisheries management to the individual level must be avoided. While it can be shown that individuals affect social organizations, it can also be shown that other organizations can influence individual behaviour.

CONCLUDING REMARKS

> Management plans based on the soundest of biological information fail when it is discovered that fishing pressure cannot be controlled because of unforeseen political or economic constraints. Economic policies fail when unforeseen biological limits are exceeded. In short, fisheries represent dynamic (time-varying) systems with interacting components.
> (C.J. Walters, Systems principles in fisheries management, 1980.)

In the fisheries literature there appear to be many unquestioned assumptions about the linkages between society and fish populations. Upon closer scrutiny, some of these assumptions take on the appearance of half-truths or "fish myths," because they prove to be valid in some circumstances but invalid in others. In this section, the issue of fish myths is raised and briefly discussed, linking different myths to each of the levels of anaylsis presented earlier.

International-level fish myths

At the international level, there appears to be an impression that a collapse of a fishery will have little effect, except in the marketplace, on other fisheries. Fisheries around the world are linked in indirect as well as direct ways. Some of those linkages are often subtle while others are obvious. For example, the successes in the early years of the Peruvian fishery sparked the interest of Chilean leaders in developing a fishing sector in the Chilean North. Chilean motives at that time for doing so were more directly related to relieving an employment problem in that region than they were for capitalizing on a potentially valuable marine resource (Salinas M., 1973). Recently (Fishing News International, August 1982), Chile surpassed Peru in terms of tonnage of landings and has emerged as one of the world's major fishing nations (by tonnage).

More tangible linkages can be established between the collapse of a fishery in one region and the stimulation of the development of a similar fishery in another. The Californian Pacific sardine collapse serves as just such an example. The same can be said more recently for the initiatives of the South African industrialists in the Chilean food fish sector in the Chilean North. Even within a region, there have been shifts from the exploitation of one species to the exploitation of another (e.g., anchoveta to sardine), although a modification of fishing gear is usually required. As fisheries collapse, where can the idled fishing vessels and processing plants go?

National-level fish myths

A national level fish myth alluded to in the literature is that fishing is mainly an economic activity. A fishery, however, is embedded in a larger political system and is only one subsystem that must compete with many others for the attention and support of political authorities. Unfortunately, no matter how productive that fishery might be, for example, in terms of producing foreign exchange, or in terms of generating employment, it may not be viewed as a significant sector, especially in developing countries where unemployment and underemployment may already be at relatively high levels. Kuczynski (1977, p. 4) commented on this factor, noting that

> Following the traditional pattern, export activity has tended to be liberal in its use of capital (land and equipment) and economical of employment....Employment in mining, fishmeal, and major agricultural exports in the mid-sixties did not directly account for more than 7 percent of total employment.

Fishing activities in developed countries as well as in developing countries are often heavily subsidized, sometimes in obvious ways, and sometimes in not so obvious ways. This suggests other motives for maintaining a fishery (such as nationalism and the desire to show the flag or to avoid increasing the number of unemployed), even when doing so might be economically unsound. As Gulland (1974, p. 107) noted, "Nearly all governments are now, to an increasing extent, becoming involved in the operational side of fishing--through such matters as the granting of loans, subsidies, etc." The condition of the exploited resource then becomes of secondary concern, as the more immediate needs and potential payoffs overshadow the longer-term impacts on the fish resource and those dependent on it.

Individual-level fish myths

A fish myth that is associated with the individual level of analysis is the usually implied, but sometimes stated, belief that there is one reality or one proper objective for managing a fishery. Most articles, books, and reports (including this one) address the question of objectives for fisheries management. As noted earlier, how one views a resource on which a fishery is based affects whether, how, and when that resource will be exploited. As there are many competing perceptions about the resource as well as about the interrelations among groups and among nations, there are competing realities about fisheries management. Discussions about objectives for fisheries management are often prescriptive, suggesting what the objectives ought to be. While there is one such concept that most participants in a fishery seem to support in theory, "to ensure the continuation of this substantial contribution to the...economy," their actions at the operational level often belie their words.

What is important for the understanding of why a particular fishery has been managed in a particular way is not a search for the single stated "proper" reality (usually the preservation of the resource). What is important is the acceptance of the fact that other realities come into play that represent the more immediate aims of those involved in the fishery. Those realities (or aims), more often than not, overshadow the one "proper" reality for which all profess support. Underscoring this point, Larkin (1978, p. 68) has written that

> Fisheries...have had their dismal fascinations for economists, especially because economic inefficiency, over-capitalization and subsidies are almost the common rule....But the abstractions that lead to recipes for maximizing dollar returns from a fishery as a whole do not begin to expose the many-sided considerations of the individual fisherman, nor of the politicians for whom the fishermen vote. In brief, fisheries management has to be very much concerned with human behaviour.

Societal factors can, for better or for worse, affect the management of a fishery. While some of these societal considerations do not appear to be directly related to fisheries, they do influence fisheries management.

Use of analogy

The Peruvian case study was chosen to highlight these societal factors because its fisheries have been prominent in the scientific and popular fisheries literature since the middle of the 1950's. In the 1950's and 1960's it served as an example of how to develop the capability to exploit a natural resource, but in the 1970's it has been cited as an example of what to avoid in the development of a fishery. Yet, to this author, it seems that examples of apparent success in fisheries management carry considerably more weight than examples of failures. For example, similarities are often cited when representatives of a fishery want to make a case for following the development path of an apparently successful fishery, while differences are usually highlighted by those who want to minimize the similarities between one's own fishery and a suggested analogous fishery that has collapsed.

To be sure, other fisheries might have been used as the case study of the management of shoaling pelagic fish, the notable ones being the Californian Pacific sardine fishery and the South African and South West African (Namibian) pilchard fisheries. There appear to be many similarities between these three cases that are worthy of additional research (see, for example, Glantz, 1980b).

The use of comparisons between fisheries based on similar species can be an extremely useful approach to develop an understanding of how coastal living marine resources are managed and why. The use of analogues in scientific research is not a new or recent phenomenon (e.g., Culley, 1971; Troadec et al., 1981). With respect to understanding Eastern Boundary pelagic fish reproduction, scientists (Parrish, et al., 1983) have recently called for the use of analogies, noting that

> The four major eastern boundary current regions of the world ocean (i.e., the California, Peru, Canary, and Benguela systems) appear to involve similar environmental dynamics and contain very similar assemblages of important pelagic fish species. To the extent that corresponding species in different systems function as analogues, interregional comparative studies may yield information concerning environmental effects on reproductive success that could be difficult to derive from any single regional system alone.

Analogues could be a useful methodological approach for an improved understanding of how societies interact with their physical and biological environments in general, and more specifically how they interact with fisheries. Used with care, that is, identifying explicitly the strengths and weaknesses of particular analogues, they can be a source of new insights for fisheries managers as well as for political and economic development decisionmakers. It may be instructive to keep in mind the following Chinese proverb: "To know the road ahead, ask those coming back."

Acknowledgement

I would like to acknowledge the research support and never-ending editorial assistance of Maria Krenz. Without her continued efforts, this paper could not have been written. I would also like to thank Dr. Steven Rhodes for his valuable critique of the many drafts of this paper. Dr. Linn Hammergren also deserves special mention for her careful review and critique of the manuscript, as does Karen Lynch for her constant assistance.

REFERENCES

Ahlstrom, E.H. and J. Radovich. 1970. Management of the Pacific sardine. pp. 183-194. In A Century of Fisheries in North America (N.G. Benson, ed.). Washington, D.C. American Fisheries Society Special Publication No. 7.

Banks, A.S. and W. Overstreet (eds). 1981. Political Handbook of the World, 1981. McGraw Hill, New York.

Bakun, A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean sciences in relation to living resources. Canadian J.Fish.Aquat.Sci. 39(7):1059-1070.

Bell, D. 1962. The End of Idealogy. The Free Press, New York.

Bjerknes, J. 1966. A possible response of the atmospheric Hadley calculations to equatorial anomalies of ocean temperatures. Tellus. 18(4):820-829.

Boerema, L.K. and J.A. Gulland. 1973. Stock assessment of the Peruvian anchovy and management of the fishery. J.Fish.Res.Bd.Canada. 30(12):2226-2235.

Boerema, L.K., G. Saetersdal, I. Tsukayama, J.E. Valdivia and B. Alegre. 1965. Report on the effects of fishing on the Peruvian stock of anchovy. Rome, Italy. FAO Fish.Tech.Pap. (55).

Borgstrom, G. 1972. Ecological aspects of protein feeding - the case of Peru. In The Careless Technology (M.T. Farvar and J.P. Milton, eds). The Natural History Press, Garden City, New York.

Brown, L. 1974. By Bread Alone. Praeger, New York.

Brown, W.B. 1965. Governmental measures affecting exports in Peru, 1945-1962. Ph.D. Dissertation, Fletcher School of Law and Diplomacy, Tufts University.

Caravedo Molinari, B. 1977. The state and the bourgeoisie in the Peruvian fishmeal industry. Latin Amer.Perspect. 14(3):103-121.

Caviedes, C. 1975. El Niño: its climatic, ecological, human and economic implications. The Geographical Review. 65:493-509.

___________. 1981. The impact of El Niño on the development of the Chilean fisheries. pp. 351-368. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Clark, C.W. 1973. The economics of overexploitation. Science. 181(4100):630-634.

___________. 1976. Mathematical Bioeconomics: the Optimal Management of Renewable Resources. John Wiley and Sons, New York.

___________. 1981. Bioeconomics of the ocean. Bioscience. 32(3):231-237.

Clark, W.G. 1977. The lessons of the Peruvian anchoveta fishery. CALCOFI Rep. XIX:57-63.

Crutchfield, J.A. and R. Lawson. 1974. West African marine fisheries - alternatives for management. Resources for the Future. Washington.

Culley, M. 1971. The Pilchard: Biology and Exploitation. Pergamon Press, Oxford.

Cushing, D.H. 1974. A link between science and management in fisheries. Fish.Bull.U.S. 72(4):859-864.

___________. 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge.

Dasmann, R.F. 1972. Environmental Conservation (3rd ed.). John Wiley and Sons, New York. pp. 313-316.

Downer, S. 1980. Even the anchovetas are returning to Peru. Euromoney (April):xi-xvi.

Easton, D. 1965. A Systems Analysis of Political Life. John Wiley and Sons, New York.

Edwards, R. and R. Hennemuth. 1975. Maximum yield: assessment and attainment. Oceanus. 18(2):3-9.

Eleguera, M. 1964. California and the World Ocean. Governor's Conference on California and World Oceans, Museum of Science and Industry, Los Angeles, CA.

FAO. 1968. State of World Fisheries. FAO, Rome, Italy.

____________. 1974. Summary of Principle Documentation, UN World Food Conference. Rome, Italy: CSD/74/34.

____________. 1979a. Interim Report of the ACMRR Working Party on the Scientific Basis of Determining Management Measures. Rome, Italy. FAO Fish.Circ. (718).

____________. 1979b. ACMRR Working Party on the Scientific Basis of Determining Management Measures, Hong Kong, 10-15 December 1979. Rome, Italy. FAO Fish.Rep. (236).

____________. 1981a. Review of the State of World Fishery Resources. Rome, Italy. FAO Fish.Circ. (710).

____________. 1981b. Comprehensive programme of assistance in the development and management of fisheries in economic zones (several brochures). FAO, Rome, Italy.

Farvar, M.T. and J.R. Milton (eds). 1972. The Careless Technology. Natural History Press, Garden City, New York.

Firth, F.E. (ed.). 1969. The Encyclopedia of Marine Resources. Van Nfptrand Reinhold, New York. pp. 509-513.

Freyre, A. 1965. Fishery development in Peru. pp. 391-411. In Proceedings of the International Conference on Tropical Oceanography.

Galtung, J. 1971. A structural theory of imperialism. J.Peace Res. 8(2):81-117.

Garcia, R. 1981. Drought and Man: the 1972 Case History, Vol.1. Nature Pleads Not Guilty. Pergamon Press, Inc., New York.

Glantz, M.H. 1979. Science, politics and economics of the Peruvian anchoveta fishery. Marine Policy. 3(3):201-210.

____________. 1980a. Man, state and the environment: An inquiry into whether solutions to desertification in the West African Sahel are known but not applied. Canadian J.Dev.Studies. 1(1):75-97.

____________. 1980b. El Niño: Lessons for coastal fisheries in Africa? Oceanus. 23(2):9-17.

Glantz, M.H. and J.D. Thompson (eds). 1981. Resource Management and Enviornmental Uncertainty: lessons from coastal upwelling fisheries. Wiley-Interscience, New York.

Golden, F. 1983. Tracking that crazy weather. Time. (April 11):67.

Goodsell, C.T. 1974. American Corporations and Peruvian Politics. Harvard University Press, Cambridge, MA.

Gould, J.R. 1972. Extinction of a fishery by commercial exploitation: A note. J.Pol.Econ. 1031-1037.

Goulet, D. 1977. The Uncertain Promise: value conflicts in technology transfer. IDOC/North America, Inc., New York.

Gordon, H.S. 1954. The economic theory of a common property resource: The fishery. J.Pol.Econ. 62:124-142.

Gulland, J.A. 1968. Population dynamics of the Peruvian anchoveta. Rome, Italy. FAO Fish.Tech. Pap. (72).

____________. 1972. Fishery management and the needs of developing countries. pp. 175-188. In World Fishery Policy: multidisciplinary views (B.J. Rothschild, eds). University of Washington Press, Seattle.

____________. 1974. The Management of Marine Fisheries. Scientechnica Ltd., Bristol.

____________. 1977. Goals and objectives of fisheries management. Rome, Italy. FAO Fish.Tech. Pap. (166).

____________. 1979. Developing countries and the new law of the sea. Oceanus. 22(1):36-42.

Hammergren, L.A. 1981. Peruvian political and administrative responses to El Niño: Organizational, ideological and political constraints on policy change. pp. 317-350. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Hardin, G. 1968. The tragedy of the commons. Science. 162:1243-1248.

____________. 1975. Land reform and social conflict in Peru. pp. 220-253. In The Peruvian Experiment (A.F. Lowenthal, ed.). Princeton University Press, Princeton, New Jersey.

Hardin, G. and J. Baden (eds.). 1977. Managing the Commons. W.H. Freeman Press, San Francisco.

Horna, H. 1968. The fish industry of Peru. J.Devel.Areas. 2(2):393-406.

Hunt, S. 1975. Direct foreign investment in Peru: new rules for an old game. pp. 302-349. In The Peruvian Experiment (A.F. Lowenthal, ed.). Princeton University Press, Princeton, New Jersey.

IMARPE. 1970. Panel of experts' report on the economic effects of alternative regulatory measures in the Peruvian anchoveta fishery. Lima, Peru. IMARPE Report No.34. pp. 369-400. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Intergovernmental Oceanographic Commission. 1974. The International Decade of Ocean Exploration (IDOE) 1971-1980. Tech.Ser. No.13. UNESCO, Paris.

Jaquette, J.S. 1975. Belaunde and Velasco: On the limits of ideological politics. pp. 402-438. In The Peruvian Experiment (A.F. Lowenthal, ed.). Princeton University Press, Princeton, New Jersey.

Kaczynski, W. 1979. Problems of long-range fisheires. Oceanus. 22(1):60-66.

Kasahara, H. 1979. Some thoughts on management. In Interim Report of the ACMRR Working Paty on the Scientific Basis of Determining Management Measures. Rome, Italy. FAO Fish.Circ. (718).

Katz, A.L. 1973. The Unusual Summer of 1972. Translated by L.A. Hutchinson, Gidrometeorizdat, Leningrad, USSR.

Kesteven, G.L. 1981. Aid in research into fishery resources: An examination of experience in aid projects executed in Mexico, Peru, Chile, Argentina, Uruguay and Venezuela. In Working Party on the Promotion of Fishery Resources Research in Developing Countries. Rome, Italy. FAO Fish.Rep. (251).

Klee, G.A. (ed.). 1980. World Systems of Traditional Resource Management. John Wiley and Sons, New York.

Kluckhohn, F.R. and F.L. Strodtbeck. 1961. Variations in Value Orientations. Row, Peterson and Co., Evanston, Illinois.

Kolhonen, J. 1974. Fish meal: International market situation and the future. Mar.Fish.Rev. 36(3):36-40.

Kuczynski, P.-P. 1977. Peruvian Democracy under Economic Stress. Princeton University Press, Princeton, New Jersey.

___________. 1981. The Peruvian external debt. J.Interamer.Stud.World Affairs. 23(1):3-27.

Larkin, P.A. 1978. Fisheries management - An essay for ecologists. Ann.Rev.Ecolog.Syst. 9:57-73.

Lees, R. 1969. Fishing for Fortunes. Purnell, Cape Town, South Africa

Levin, J.V. 1960. The Export Economies. Harvard University Press, Cambridge, MA.

MacCall, A.D. 1983. Variability of pelagic fish stocks off California (mimeo, National Marine Fisheries Service, Southwest Fisheries Center).

Malpica, C. 1975. Anchovetas y Tiburones. Lima, Peru.

Marx, W. 1967. The Frail Ocean. Ballantine Books, New York.

___________. 1981. The Oceans: Our Last Resource. Sierra Club Books, San Francisco.

Massey, P. 1972. Is fishmeal a threat to Peru's guano birds? Peruvian Times Fisheries Supplement: 32-37.

Miller, F.R. and R.M. Laurs. 1975. The El Niño of 1972-1973 in the eastern tropical Pacific Ocean. Bull.Inter-Amer.Trop.Tuna Comm. 16(5):403-416.

Miller, R., C.T. Smith and J. Fisher (eds). 1974. Social and Economic Change in Modern Peru. Liverpool, U.K. Centre for Latin-American Studies, Monograph Series No. 6.

Ministry of Fisheries, Peru. 1977. Report of Consultative Group on the State of the Stocks of Anchoveta and Other Pelagic Species and on the Courses of Action to be Taken for Management of the Fishery. Lima, Peru (July).

Murphy, G.I. 1977. Clupeoids. pp. 283-308. In Fish Population Dynamics (J.A. Gulland, ed.). Wiley-Interscience, New York.

Murphy, R.C. 1926. Oceanic and climatic phenomena along the west coast of South America during 1925. Geograph.Rev. 13:64-85.

___________. 1954. El guano y las pesca de anchoveta (Guano and the anchoveta fishery). Official report of the Compañía Administradora del Guano to the National Government, Lima, peru. pp. 81-106. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Murphy, R.C. and G.E. Barstow Murphy. 1959. Peru profits from sea fowl. National Geographic, CXV, 3 (March):395-413.

National Research Council. 1982. An ocean-atmosphere climatic interaction study: El Niño and the Southern Oscillation (ENSO). Draft report, October 15, 1982, NRC Climate Research Committee. National Academy of Sciences, Washington, D.C.

O'Brien, J.J. 1978. El Niño: an example of ocean/atmosphere interactions. Oceanus. 21(4):40-46.

O'Brien, J.J., A. Busalacchi and J. Kindle. 1981. Ocean models of El Niño. pp. 159-212. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Olson, R.S. 1975. Economic coercion in international disputes: The U.S. and Peru in the IPC expropriation dispute of 1968-1971. J.Develop.Areas. 9:395-414.

Padelford, N.H. and G.A. Lincoln. 1962. Dynamics of International Politics. Macmillan, New York, 23 p..

Parrish, R.H., A. Bakun, D. Husby and S. Nelson. (This volume). Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction.

Paulik, G.J. 1971. Anchovies, birds and fishermen in the Peru Current. pp. 156-185. In Environment, Resources, Pollution and Society (W.W. Murdock, ed.). Sinauer Press, Stamford, CT.

Philander, S.G.H. 1983. El Niño Southern Oscillation phenoma. Nature. 302(5906):295-301.

Popiel, J. and J. Sosinski. 1973. Industrial fisheries and their influence on catches for human consumption. J.Fish.Res.Bd.Canada. 30:2254-2259.

Posner, G.C. 1957. The Peru Current. Bull.Bingham Oceanogr.Coll. XVI. Yale University Museum, New Haven. pp. 106-153.

Pulgar Vidal, J. (no date). Geografía del Peru (2nd ed.). Editorial Universo, Lima, Peru.

Quinn, W.H. 1984. (In press). El Niño. In Encyclopedia of Climatology (J.E. Oliver, ed.). Hutchinson Ross Publishing Co., Stroudsburg, PA.

Radovich, J. 1981. The collapse of the California sardine fishery: what have we learned? pp. 107-136. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Ramage, C. 1975. Preliminary discussion of the meteorology of the 1972-73 El Niño. Bull.Amer. Meteor.Soc. 56(2):234-242.

Rasmusson, E.M. and T.H. Carpenter. 1982. Variations in tropical sea surface temperature and surface wind fields associated with the southern oscillation/El Niño. Mon.Weather Rev. 110:354-384.

Reinstedt, R.A. 1978. Where Have all the Sardines Gone? Ghost Town Publications, Carmel, CA.

Robinson, M.A. 1980. World fisheries to 2000: supply, demand and management. Marine Policy (January):19-31.

_____________. 1982. Prospects for World Fisheries to 2000. Rome, Italy. FAO Fish.Circ. (722).

Roemer, M. 1970. Fishing for Growth. Harvard University Press, Cambridge, MA.

Rothschild, B.J. 1973. Questions of strategy in fishery management and development. J.Fish.Res. Bd.Canada. 30(12):2017-2030.

Salinas, M.R. 1973. The fishmeal industry of Iquique. In Coastal Deserts (D.H.K. Amiran and A.W. Wilson, eds). The University of Arizona Press, Tuscon, AZ.

Schaefer, M.B. 1967. Dynamics of the fishery for the anchoveta Engraulis ringens off Peru. Instituto del Mar del Peru. Bol. 1(5):189-304.

Schärfe, J. 1979. Fishing technology for developing countries. Oceanus. 22(1):54-59.

Smetherman, B.B. and R.M. Smetherman. 1972. Peruvian fisheries: conservation and development. Econ.Devel.Cult.Change. 21(2):338-351.

Smith, R.L. 1968. Upwelling. pp. 11-46. In Oceanography, Marine Biology, Annual Review (H. Barnes, ed.). George Allen and Unwin, London.

South African Journal of Science. 1980. A critique of "The control of a pelagic fish resource". 76 (October):453-466.

Spring, D. and E. Spring. 1974. Ecology and Religion in History. Harper and Row, New York.

Stroetzel, D.S. 1965. Fishing for meal. The Americas. (May):18-22.

Tantaleán Vanini, J. 1978. Yo Respondo. Lima, Peru.

Thompson, J.D. 1977. Ocean deserts and ocean oases. In Desertification: environmental degradation in and around arid lands (M.H. Glantz, ed.). Westview Press, Boulder, Colo.

Tomczak, M., Jr. 1981. Prediction of environmental changes and the struggle of the Third World for national independence: the case of the Peruvian fisheries. pp. 401-435. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Tovar, H. (This volume). Fluctuaciones de poblaciones de aves guaneras en el litoral Peruano, 1960-1981.

Traeger, J. 1975. The Great Grain Robbery. Ballantine, New York.

Troadec, J.-P., W.G. Clark and J.A. Gulland. 1980. Draft. A review of some pelagic fisheries in other areas. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:252-277.

Tropical Oceanographic-Atmospheric Newsletter. 1983. Special issue, February 1983.

U.S. National Weather Service. 1982. A major warm episode in the Eastern Equatorial Pacific Ocean. Special climate diagnostics bulletin, mimeo, 82/2.

Valdez-Zamudio, F. 1973. Impacto de medidas regulatorias en la industria pesquera peruana. J.Fish.Res.Bd.Canada. 30(12):2242-2253.

Vondruska, J. 1981. Postwar production, consumption, and prices of fish meal. pp. 285-316. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries (M.H. Glantz and J.D. Thompson, eds). Wiley-Interscience, New York.

Walters, C.J. 1980. Systems principles in fisheries management. In Fisheries Management (R.T. Lackey and L.A. Nielsen, eds). Blackwell Sci.Pub., London.

Waltz, K. 1959. Man, State and War. Columbia University, New York.

Weare, B.C. 1982. El Niño and tropical Pacific Ocean surface temperatures. J. of Physical Oceanogr. 12:17-27.

Wilbur-Ellis. 1972. Wilbur-Ellis Company: The First Fifty Years, 1920-1971. Wilbur-Ellis Co., New York.

Wooster, W.S. and O. Guillén. 1974. Characteristics of El Niño in 1972. J. of Marine Res. 32(3):387-404.

Whyte, W.F. and G. Alberti. 1977. The industrial community in Peru. Annals of the American Academy of Political and Social Science. 431:103-113.

Wyrtki, K. et al. 1976. Predicting and observing El Niño. Science. 191:343-346.

SCIENCE AND DECISION-MAKING IN FISHERIES REGULATION

by

Ray J.H. Beverton

International Federation of Institutes
for Advanced Study (IFIAS-ABC)
55 Sandown Avenue
Swindon, Wilts SN3 1 QQ
United Kingdom

Resumen

Se comentan algunos de los problemas que se encuentran al tratar de entender mejor la relación entre la ciencia y la toma de decisiones en la explotación de recursos pesqueros. Los conceptos sobre rendimiento máximo sostenible, la teoría del rendimiento de equilibrio y la ordenación pesquera se consideran como aspectos fundamentales en la comunicación entre estos dos sectores y se discuten en esta perspectiva. Se hace referencia en los distintos factores que deben ser tomados en cuenta para poder hacer un enfoque socio-económico integral al sistema pesquero y se intenta una primera clasificación del riesgo de explotación. Se discuten también algunas de las implicaciones que deben ser tenidas en cuenta en el proceso de toma de decisiones.

INTRODUCTION

Having been for a decade or so away from the mainstream of fisheries research, I am not infrequently asked what I make of events during that time (i.e. from 1965 to 1980, give or take a year or so). Sometimes the question is accompanied by the comment - you will no doubt have noticed that the same old problems are still with us. It is, indeed, a somewhat sobering thought that the theme of this Conference - except for its geographical slant and the word 'neritic' - could well have been that of an ICES Special Meeting as far back as the 1930's.

As is true of so much human endeavour, progress in fisheries research has been like the curate's egg - good, in parts. Our understanding of some aspects of the ecological basis of fish populations has advanced greatly, as have our techniques for sampling and analysis of data. No less spectacular have been the theoretical developments, and I scan modern fisheries mathematics with awe and a large degree of incomprehension.

The accumulating stock/recruitment data have provided a bonanza for the curve-fitters, an activity which has attracted some justified scepticism. Nevertheless, we really do know a great deal more about the relationship between parent and progeny in fish populations than when Sidney Holt and I at Lowestoft and Bill Ricker at Nanaimo were trying to extract the last ounce of information from the limited data we then had. The high variability of S/R data may be 'noise' to the statistician but to the biologist it should hold the secret to much of what we want to know about fisheries - if he knows where and how to look for it. The fact remains, however, that we still have only clues here and there as to the environmental causes of recruitment fluctuations, and even less of the natural compensatory mechanisms, if any, in the major marine fish populations.

Perhaps these "failures", if that is a correct description, have been at least partly responsible for what seems to me to have been a more disturbing development in the last decade. I refer to the crisis of confidence which has built up in some quarters concerning the fundamental validity of the scientific basis for fisheries management. These doubts have been eloquently expressed by some of the leading fisheries scientists of my, as well as the younger, generation. The concept of maximum sustainable yield (MSY) as the objective of management has come in for particularly strong criticism (e.g. Larkin, 1977); Holt (1980) goes further, challenging the whole idea that man can "manage" living marine resources on scientific principles.

In view of the surprises and disappointments of recent years this reaction is understandable. Nature has a way of giving us embarrassing reminders of how easily our best laid plans can come unstuck; fisheries is no exception, especially when some of our plans have not been that well laid. But that does not mean for a moment that a rational approach to the utilisation of our fish resources is not possible or necessary, or that science does not have a major role to play. Whatever the frailties in fisheries science and management that may have been exposed by recent events, the destructive power of unrestrained modern fishing operations, backed by economic and political pressure, has become only too painfully obvious.

Not the least of the problems that are still with us, perhaps even more acutely, is that of communicating scientific assessments of fisheries to the decision-makers. This paper is offered as a small contribution towards finding a way forward in this grey area, which necessarily involves the socio-economic dimension and the treatment of uncertainty and risk. It extends certain concepts I put forward in the Santiago seminar of August 1982 co-sponsored by FAO and IOC (Beverton, in press); and draws in particular on the chapter on the Societal Value of an El Niño forecast, by Michael Glantz, in Resource and Environmental Uncertainty; John Wiley, 1981.

MANAGEMENT AND MSY

It is frequently claimed that the concepts of MSY and equilibrium yield theory are obsolete. This issue is central to the communication between science and decision-making, as is the concept of "management" of fisheries: it is worth checking on where we stand, and return later.

In my time we did not use the word "management" nor the term MSY. I was brought up in the Michael Graham school of "rational exploitation". By this was meant harvesting (the agricultural analogy was intended) the natural productivity of the fish stocks in a sensible way, i.e. letting fish grow to a reasonable size before catching them, and not making the future worse by wasting time and money fishing unnecessarily hard. In view of the intrinsic tendency to the contrary in any common property resource, we thought primarily of "regulation", i.e. a means of restraining this otherwise inevitable drift of the fishery towards self-immolation, rather than the more positive and comprehensive control conjured up by the word "management".

The equilibrium yield theory as Sidney Holt and I developed it, both as yield per recruit and as absolute yield incorporating a stock-recruitment relationship, was intended to formalise this principle of fisheries regulation and provided a basis for action. Fig. 1 illustrates this approach. We worked on the premise that if the equilibrium yield curve had a maximum (at F_{max}) and if the present F_1 was manifestly higher than that, then more of the potential natural productivity of each cohort would be utilised at less cost if F were reduced to F_{max} and kept there, or thereabouts.

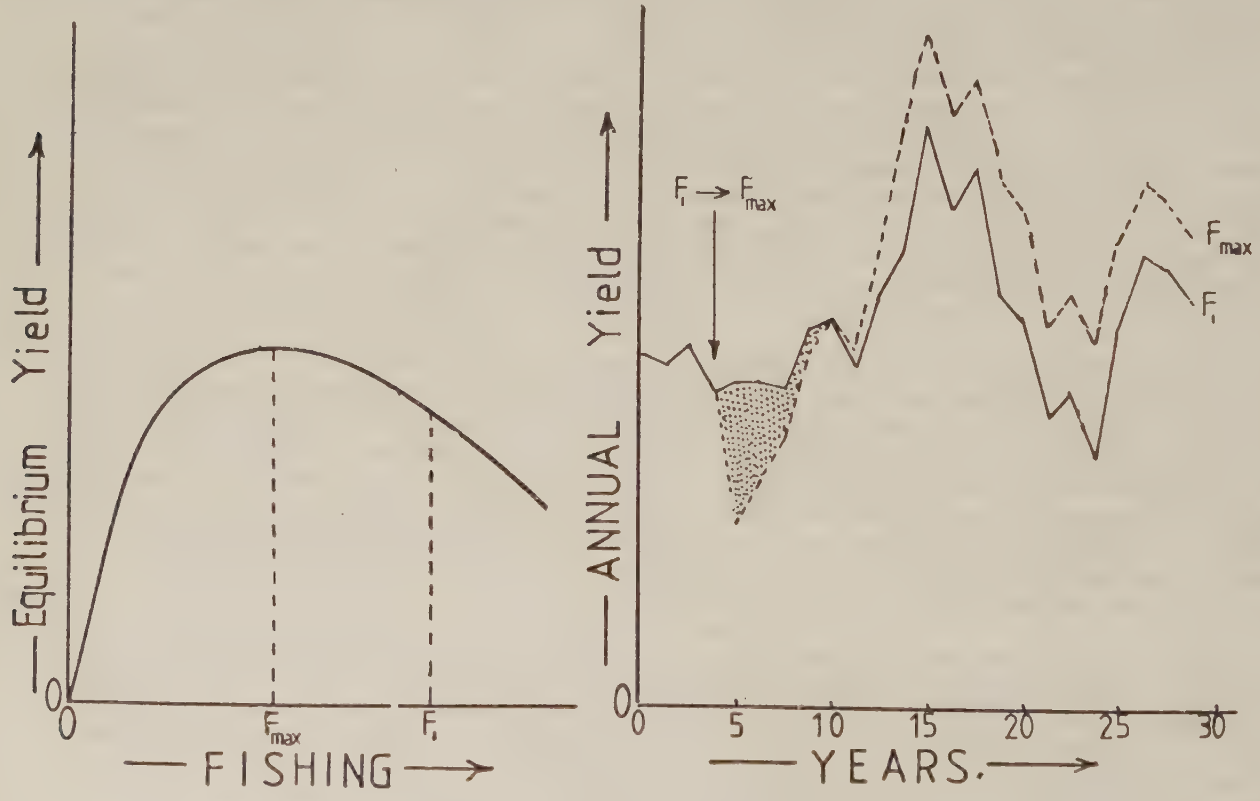


Fig. 1. Hypothetical illustration of relative improvement by regulation of fishing effort, F being reduced from F_1 to F_{max}.

Depending on how that reduction was brought about so, we supposed, would the long-term economic situation be improved (by most criteria). Future recruitment, and hence catches, would of course continue to fluctuate, as they always had, for reasons beyond man's control. We did not attempt to forecast what actual catches would be in the future. We simply said that if F were reduced (or age at first capture increased, e.g.

by a larger mesh) then catches (and catch per unit effort even more so) would be that much greater than they would have been had the reduction in F (or increase in mesh) not been made. Admittedly, this was not an easy option to sell to the industrial decision-makers, even though the resultant marginal gain (provided it was not dissipated in other ways) could have made all the difference between a weak and a strong fishing economy. But it was a start.

The concept of Maximum Sustainable Yield (MSY), in absolute units, as the prime objective of fisheries management, arose I believe during the 1960's in response to a need for simple legal definition. MSY seems at first sight simple, practical and politically neutral, with catch limits as the means of control. The criticism of the economists that MSY would rarely coincide with the conditions for maximising economic rent was valid but not an overriding objection, at least for fisheries which were already overfished. In fact, by redefining the objective as actual maximum yield instead of the operational requirements (fishing rate and selectivity) for achieving a more rational exploitation, the rules of the "management game" became subtly but fundamentally altered. "Sustainable" became synonymous with "steady", and success or failure of management became linked with the much more demanding - usually impossible - task of maintaining a constant catch rate despite often extreme natural fluctuations. The fisheries biologist, for one, was in trouble.

Whether this explains the drift into the more ambitious concept of "management" instead of "regulation", with man as the benign controller of the natural systems (and, by implication, of the socio-economic counterpart also), I do not know. If it does, then care is needed if we are to carry the confidence of the decision-makers with us in dealing with any but the simplest and most stable of fishery conditions.

Density-dependent complications, including stock/recruitment, may modify but do not invalidate the equilibrium or "average expectation" concepts, provided one can work on a long-term basis and accept variation in recruitment as part of the game. There are, however, some clear limitations to this approach, among them:

(a) policy for fisheries in the early stage of development. Caddy (1983) gives a good analysis of these non-equilibrium situations, as do Sharp, Csirke and Garcia (this volume).

(b) policy for fisheries which exist in unstable oceanographic conditions, with major periodic or episodic perturbations, as exemplified by the Peruvian anchovy and Californian and Japanese sardine.

(c) policy for fisheries which are liable to collapse under heavy fishing, as exemplified by the North Sea and Atlanto-Scandian herring.

In all these cases biological assessment alone is not sufficient. Decisions are, or ought to be, made on a trade-off between possible gains and losses measured in different units and different time-scales. Some aspects of socio-economics, and probably politics as well, must therefore be allowed for. How and by whom is for consideration.

INTRODUCTION OF SOCIO-ECONOMICS: THE TOTAL FISHERY SYSTEM

The factors to be taken into account in addition to those used in conventional fishery assessment will depend very much on the circumstances, but a general list might include the following:

1. Prospects in alternative stocks and "costs" of switching.
2. Costs of fishing, capital and recurrent.
3. Shore facilities, storage and transport.
4. Markets, demand and prices.

5. Availability and skill of manpower.
6. Alternative commodities, e.g. frozen foods other than from the sea.
7. Overall financial prospects; loans etc., national and international.
8. Administrative and legal policy at national and international level.

It would be possible, but unhelpful, to represent the interactions between these and the physico-biological fishery sub-system by drawing a multitude of boxes linked by a network of lines and arrows. I am, however, indebted to my colleague Professor Rolando Garcia 1/ for pointing out to me that this kind of socio-economic system does have a general structure which can be represented for analysis in terms of processes happening at three levels of integration, characterised by their dimensions of space and time and by the extent to which they are influenced by factors external to the system itself. I have found that the same kind of 3-level structure can be used to represent the physico-biological part of the fishery system, the two being linked at one level only (see also Glantz, this volume).

Fig. 2 represents the physico-biological and socio-economic limbs of the overall fishery system on these principles, much of which is self-explanatory. As it stands, this does not solve anything, but it may help to clarify ideas because it shows that certain "rules" must be followed in attempting to bring socio-economics into the picture. Thus,

(a) The only direct interaction between the two sub-systems is at the "hinge of the book", between levels 1A and 1B. This interaction consists of the flow of fish caught, from 1A→1B, which is soon transformed into its monetary equivalent; and of time, hardware, and skills via the operations of the fishing fleet in the other direction 1B→1A (also with a monetary equivalent).

(b) Materials, animate and inanimate, and "influence" in the form of "decisions", flow across both pages into the hinge, i.e. 3→2→1. By means of loops and feedbacks, there is a reverse interaction - more limited (absent 2A→3A) but in some cases critical in determining the dynamics of at least the immediately adjacent levels.

(c) Conventional fishery assessments establish the functional relationships across the boundaries 2A⇌1A⇌1B. Occasionally, if economic considerations are involved, they extend to level 2B in a limited way.

(d) Cross-flow of materials and "influence" between the pages without going through the hinge is permissible only by introducing a wholly new factor into the system. For example, if the stocks are replenished by some form of cultivation, the link would go from the appropriate B level (either 2B or 3B) into level 3A (nutrients), 2A (eggs and larvae) and 1A (post-recruit fish). The diagram reminds us that the effect on the overall system could not be assessed unless the input level is specified and the inter-level interactions towards the hinge (3A→2A→1A) are known.

(e) In contrast, information about the physico-biological system does pass direct to various levels in the socio-economic sub-system (i.e. between the pages), with or without the scientific interpretation. The timeliness and competence of that information flow obviously has a major influence in the fluctuations of the overall system.

This representation of the interlocking between the physico-biological and the socio-economic components of the total fishery system cannot show explicitly the dimension of time which characterises the various flows and feedbacks. This aspect, and especially the occurrence and consequences of time-lags in the dynamics of fisheries, is well analysed by Caddy. It will not be further mentioned here except to observe that time-lags in the socio-economic sub-system, just as in the physico-biological sub-system, apply at various levels and have analogous and often control effects on the dynamics of the overall system.

1/ Head of Dept. of Epistemology at the Metropolitan University of Mexico City: formerly Dean of Sciences at University of Buenos Aires and Director of the Argentinian Meteorological Service. In Drought and Man, Pergamon Press, 1982 and pers. comm.

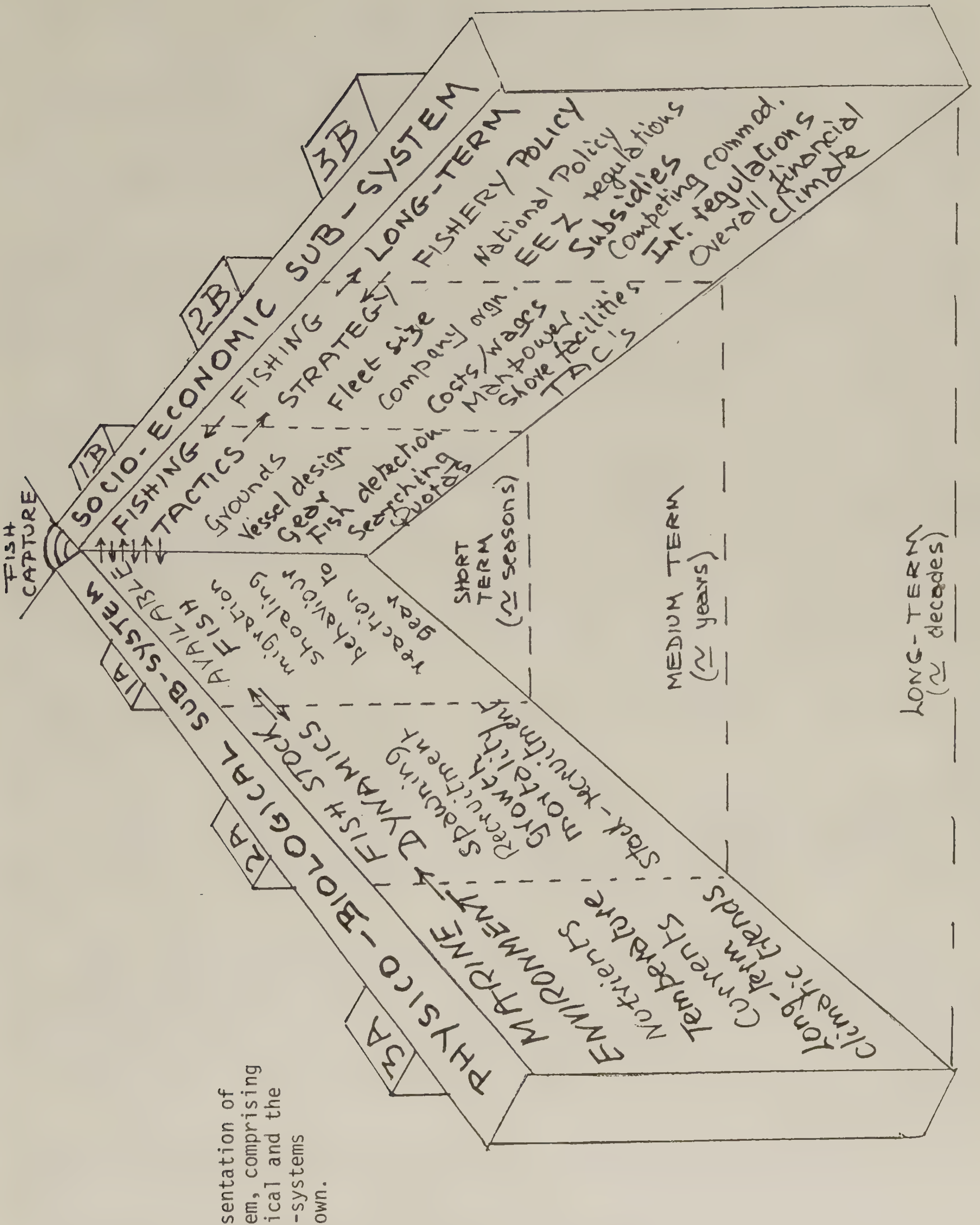

FISH CAPTURE
SOCIO-ECONOMIC SUB-SYSTEM
1B
2B
3B
FISHING TACTICS
FISHING STRATEGY
LONG-TERM FISHERY POLICY
Grounds
Vessel design
Gear
Fish detection
Searching
Quotas
Fleet size
Company orgn.
Costs/wages
Manpower
Shore facilities
TAC's
National Policy
EEZ regulations
Subsidies
Competing commod.
Int. regulations
Overall financial climate
PHYSICO-BIOLOGICAL SUB-SYSTEM
1A
2A
3A
AVAILABLE FISH
migration
shoaling
behaviour of
reaction to gear
FISH STOCK DYNAMICS
Spawning
Recruitment
Growth
mortality
Stock-recruitment
MARINE ENVIRONMENT
Nutrients
Temperature
Currents
Long-term trends
climatic
SHORT TERM (≃ seasons)
MEDIUM TERM (≃ years)
LONG-TERM (≃ decades)

Fig. 2.

Diagrammatic representation of total fishery system, comprising the physico-biological and the socio-economic sub-systems interlocking as shown. See also text.

CLASSIFICATION OF "EXPLOITATION RISK"

The decline, collapse and even recovery, of major fisheries in recent decades, for whatever reason, immediately raises a number of fundamental questions for the decision-makers. Those with which I am concerned here center around the questions:

(a) Could such events have been forecast in real time; and if so, for how long ahead, with what reliability and what is the diagnostic evidence?

or if that is not possible; -

(b) Could the possibility of collapse at some time have been anticipated from the characteristics of the fishery; and if so, what are these characteristics?

These questions are valid even if MSY is not the objective, since they strike at the root of the stability of the fishery industry, to maintain which must surely be a priority objective of management in almost all circumstances. What can we offer the decision-makers on this?

Regulation by catch quotas has made it necessary to have estimates of future year class strength as far ahead as possible. In practice this usually means 1-3 years depending on the length of the pre-exploited phase and the feasibility of estimating reliably the abundance of the pre-recruits. This might help tactical decision-making (i.e. at level 1B of Fig. 2), but is insufficient for decisions on commitment of major capital resources at high levels. In the present state of knowledge we must discount the practical possibility of making 'real-time' forecasts of future year-classes from oceanographic conditions, except in special cases (of which the El Niño phenomenon may be one). Nevertheless, we ought to be able to say something from experience about the risk involved in exploiting the main types of stocks and associated fisheries.

It was this line of thinking that led me to attempt such a classification for the Santiago conference. Caddy[2] has been working on the same lines and cites Kawasaki (1979) similarly. The latter confines his criteria to biological characteristics of the stock, but this is only part of the story. Caddy groups fisheries into several categories primarily on the basis of the historical pattern of trends and periodicities in catches, together with a knowledge of the environmental stability. This makes for a better diagnosis, but trends and fluctuations in catch alone can be very misleading, as recognized by Caddy, especially in mixed fisheries when effort can switch from one species to another or is affected by external events such as fishery restrictions or economic factors.

I believe, however, that a further development of this approach is possible and potentially useful to the decision-maker in devising his medium to long-range fishery strategy in both new and established fisheries. It is best visualised with reference to the overall fishery system represented in Fig. 2. Instability can be generated in or between any levels in either the physico-chemical or the socio-economic sub-system, or, more especially, at the interaction between the two main sub-systems (e.g. at the spine of the 'book' of Fig. 2). The more critical of these potential sources of instability would seem to be the following:

(a) environmental conditions as they affect the integrity of the life-cycle, as manifest notably but not exclusively by the variability of recruitment (1A→2A).

(b) degree of compensation in the generation-to-generation transfer, i.e. in the stock-recruitment relationship, as mediated through the life-time dynamics (growth, mortality and maturation) of each cohort (2A⇄1A).

(c) behaviour of individual fish; particularly their shoaling propensities, detectability and use of habitat protection from fishing activity (1A).

2/ J.F. Caddy An alternative to Equilibrium Theory for Management of Fisheries. FAO Expert Consultation on the Regulation of Fishing Effort, 1983.

(d) efficiency of fishing operations; particularly fish detection technology, group searching tactics and capacity to switch to alternative species (1B).

(e) elasticity of supply and demand, market preferences, mobility of capital investment (1B$\rightleftarrows$2B).

(f) long-term status of the fishing industry in the national economy; competing products, responsiveness of the regulative framework (2B$\rightleftarrows$3B).

Application of the first four of these criteria to characterise six well-documented fisheries in terms of "exploitation risk" is shown in Table 1, taken from Beverton (in press). The additional socio-economic factors (e) and (f) in the above list have nothing to do with the fish resources as such, but in certain circumstances could be important destabilisation factors and certainty would be, or ought to be, taken into account by the decision-makers.

Commenting in turn on the first four criteria, several kinds of environmental characteristics can be identified from experience as having been instrumental in causing or triggering dramatic fishery changes in stocks living at the extremes of their range which are likely to be most susceptible. Thus, the warming of the North Atlantic in the 1920's was followed by the rise of the West Greenland cod fishery (at the northern limit of the range of the species, *Gadus callarias*) the disappearance of the Plymouth herring fishery (at the southern limit of the range of the herring) (*Clupea harengus harengus*) and its replacement in the English Channel by the pilchard (*Sardinops pilchardus*) spreading northwards from further south. (See Beverton, R.J.H. and Lee, A.J., 1965). Stocks living in or close to a major current system are clearly in an uncertain environment, as instanced by the virtual disappearance of the Japanese sardine (*S. melanosticta*) in the 1940's, following changes in the course of the Kuroshio current in which it had previously spent the early part of its life-history (Kondo, 1980). Again, the precarious state of stocks living in upwelling systems, e.g. the California sardine (*S. sagax caerulea*) and the Peruvian anchovy (*Engraulis ringens*) is well established (see, e.g. Glantz, et al., ibid.).

The degree of compensation in the stock-recruitment relationship, i.e. the extent to which recruitment remains effectively independent of stock size, has a powerful effect on the stability of the fishery. As a general guide, those species that spend part of their early life-history in shallow, confined nursery areas (typified by flatfish in temperate regions) are likely to show high compensation (Ursin, 1982). A much better diagnosis is possible if good stock-recruit data are available. No sophisticated theory or curve-fitting is needed to bring out the high degree of compensation in the stock-recruitment arrays shown in Figs. 3 (a), (b) and (c) for the North Sea sole (*Solea solea*) and herring compared with the weakly compensated Peruvian anchovy. Trends in catches are shown also for comparison. Yet although both the sole and herring have been heavily fished only the latter has collapsed--so far, at least. Strong compensation, though necessary for stability, is evidently not a sufficient protection on its own.

Criteria (c) and (d) provide the clue. The sole is a demersal species which can remain partially buried in the sea-bed; it does not shoal and is undetectable by sonar. All these characteristics mediate the extreme impact of fishing but are not possessed by herring. Explicit proof of a tendency for the catchability coefficient q to increase as stock size declines is not easily demonstrated for the North Sea herring, since a variety of gears have been used in the years (see, e.g. Pope, 1980). There is, however, strong inferential evidence that it does, since a nearly hyperbolic function of q with stock size has been found in several other purse-seine fisheries for pelagic species, notably by Ulltang (1980) for the Norwegian spring spawning herring, by MacCall (1976) for the California sardine and by Butterworth (this volume) for the South West African pilchard.

It is not difficult to see how a nearly hyperbolic relationship between q and stock size, acting synergistically with the other criteria listed above, can lead to virtual certain collapse for a fishery unless drastic remedial action is taken, and in time. Fig. 4 is a simple representation of this positive feed-back system. Suppose that a fishery

Table 1: Classification of exploitation prospects for six selected fisheries. (From Beverton, in press)

	NORTH SEA PLAICE	NORTH SEA HADDOCK	NORTH SEA HERRING	ATLANTO-SCANDIAN HERRING	PERUVIAN ANCHOVY	CALIFORNIA SARDINE
MARINE ENVIRONMENT	Stable	Stable	Stable	Moderately stable	Unstable (upwelling)	Unstable (upwelling)
FISH POPULATION DYNAMICS						
- Degree of S-R compensation	High	Indeterminate	Fairly high	Moderate	Low	Very low
- Variability of R	Low	Very high	Moderate	Spasmodically high	Low-Moderate	Moderate
- Life-span	Long(20+yrs)	Medium(12+yrs)	Medium(12+yrs)	Medium-Long (15+yrs)	Short(4+yrs)	Medium(10+yrs)
- Pre-mature phase	Long(3-4yrs)	Medium(2yrs)	Medium(2yrs)	Medium(2yrs)	Short(1yr)	Medium(2yrs)
- % of growth(wt) span after recruitment	Large(90%)	Large(80%)	Small(40%)	Medium(60%)	Short to Medium(50%)	Medium(50%)
FISH BEHAVIOUR						
- Habit	demersal	demersal	pelagic	pelagic	pelagic	pelagic
- Environmental "shelter"	partial	partial	none	none	none	none
- Shoaling tendency	slight	some	strong	very strong	strong	strong
- Ease of detection	undetectable	limited	easily	easily	easily	easily
- Dependence (inverse) of catchability on abundance	none	probably none	probably strong	very strong	strong	strong
- Vulnerability to escalation of F	resilient	resilient	vulnerable	very vulnerable	very vulnerable	very vulnerable
OVERALL FISHERY PROSPECTS	Steady and dependable in short and long-term	Highly erratic in short to medium-term; probably reliable in long-term	Fairly steady in short to medium-term; long-term reliability uncertain	Spasmodic; long-term reliability suspect	Unreliable in medium to long-term, with sudden changes	Unreliable; unstable in the long-term

⋙—— INCREASING EXPLOITATION RISK ——→

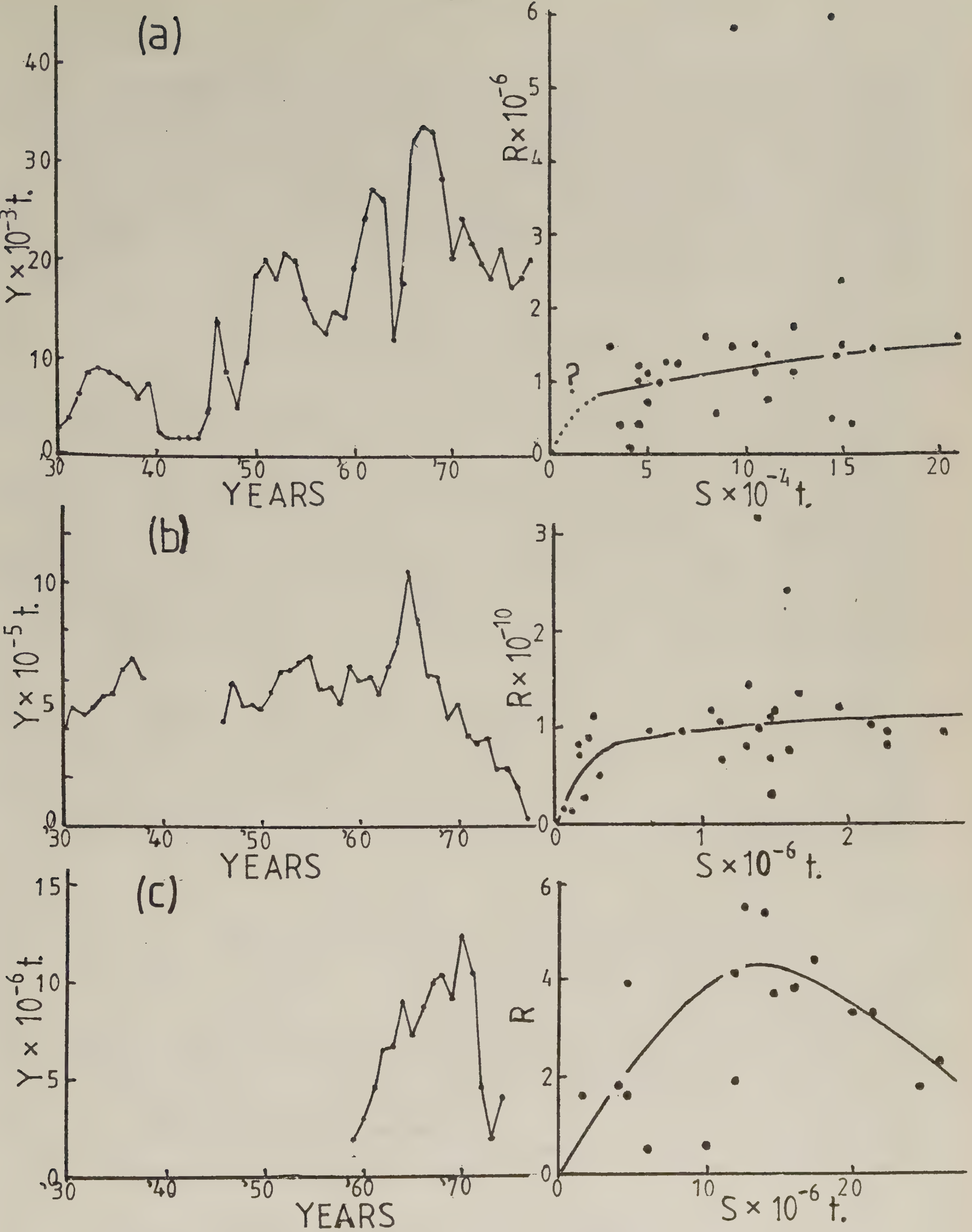


Fig. 3. Long-term trends in landings (left-hand diagrams) and the stock-recruitment arrays (right hand diagrams) for the fisheries for: (a) North Sea sole (stable) (b) North Sea herring (collapsed) (c) Peruvian anchovy (unstable). These diagrams show that neither trends in landings nor the shape of the stock-recruitment arrays is alone sufficient as a diagnosis of the stability characteristics of fisheries (see also text). Data from Garrod (1982), Saville and Bailey (1980), and Csirke (1980).

has been in a reasonably steady condition under moderate fishing for some years, generating the mean stock-from-recruit line A intersecting with the mean recruit-from-stock curve at S_1, R_1 as shown. Suppose now that a transient environmental perturbation causes recruitment to fall to r_1. This poorer year-class will cause the stock to fall which in turn will cause q to increase and steepen the recruit-from-stock line to B. The stock is now more vulnerable to a second fortuitously weak year-class r_2, which leads to a further decrease in stock and increase in q. Eventually, the stock-from-recruit line is displaced to D, at which it no longer intersects with the recruit-from-stock curve at any point. The stock now procedes to extinction unless fishing is drastically curtailed or stopped altogether.

IMPLICATIONS FOR DECISION-MAKING

In conclusion, let us consider a few of the problems posed to the decision-maker in the light of the above analysis of fishery systems, and the contribution of the scientists to their solution.

Fig. 2 illustrates the obvious point that to pass from between the two sub-systems in the direction 1A→1B requires, at the least, transformation of the key variables of effort and catch into monetary equivalents. Despite the significant contributions to fishery dynamics from the economics profession in recent years, it is not immediately apparent in the fisheries literature that any general relationships have been established between these variables. Perhaps I have been looking in the wrong place, yet much of the significance to the decision-maker of stock variability is lost, or at least greatly modified if, for example, the relationship between weight of catch and its price is strongly elastic. Gulland's (1980) analysis of long-term trends in the value of North Sea landings is one of the few of this kind and illustrates this latter point well.

The possible objectives for the management of established and reasonably "reliable" fisheries (see Table 1) have been discussed in the literature with a thoroughness not matched by the clarity with which they are usually defined in practice. It is sufficient here to observe that one way of posing the general problem starts with the premise that there is a potential maximum economic rent that could be gained over time from a fishery (on one or a complex of stocks) if it is managed appropriately. The ultimate choices then lie between:

(a) enabling that maximum rent to be realized directly as profit, which implies a firm limitation of the amount of fishing, or

(b) allowing rather more fishing so that part of that potential rent is dissipated as may be desired, e.g. in larger average catches (possibly, but only within limits), and a larger fishing community in the catching and operational sectors.

As thus formulated, choosing the objectives of fisheries management has a strong political element, to which neither the fisheries scientist nor even the economists can contribute much. There is clearly no generally applicable prescription, although wherever the fishing industry is a major factor in the natural economy or is expected to function as a fairly self-sufficient unit within the national economy, a high priority will be given to achieving a reasonable stability for the fishery system as a whole. Put in these terms, management necessarily involves some form of risk assessment in the way discussed above, with stock variability a dominant factor--and the scientist has a crucial role to play.

This point is well illustrated by returning again to the question of how to keep a fishery reasonably clear of the kind of collapses typified by the herring fisheries cited above, and the "price" to pay for what may be called "prudent exploitation". The decline of the Norwegian spring spawning herring fishery over the decade from 1960 to its eventual collapse in 1970, with the attendant changes in the size and structure of the stock, have been well documented by the scientists of the Bergen Laboratory (e.g. in Dragesund, Hamre and Ulltang, 1980; and summarised by Bakken, this symposium). This evidence provides a real-life demonstration of the sequence of events illustrated in Fig. 4.

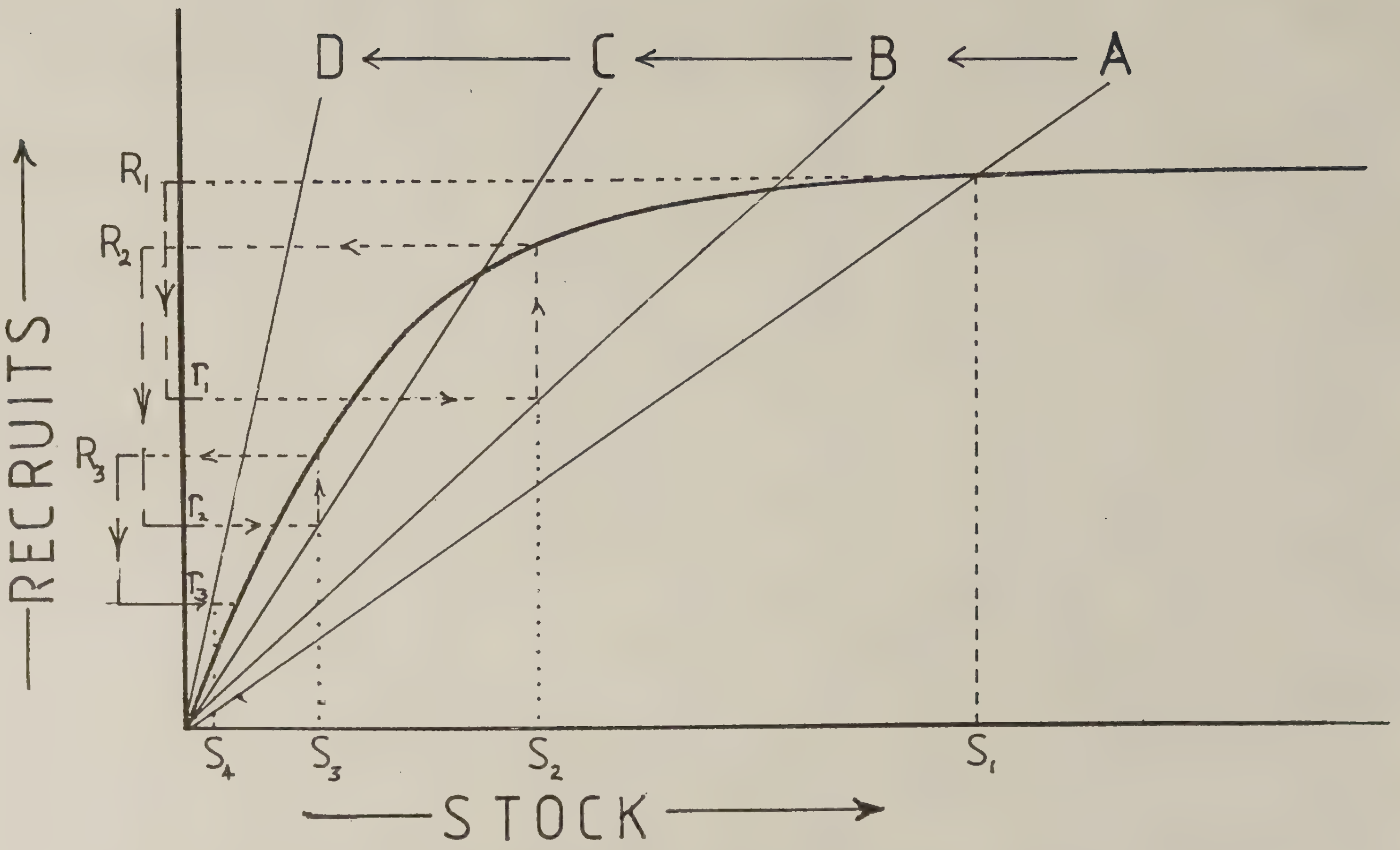


Fig. 4. Hypothetical stock-recruitment relationship to show how a succession of three poor year-classes (r_1, r_2, r_3) working through an inverse relationship between q and density, can cause a progressive increase in F and hence, steepening of the stock-per-recruit lines (A→B→C→D) resulting eventually in stock extinction (line D no longer intersecting with the recruitment-stock curve at any point). See also text.

Fig. 5 shows how F changed with stock size during this period, the rapid escalation of F at low stock levels being due not to an increase in the amount of fishing but to the nearly inverse relationship between q and stock abundance in this fishery (Ulltang, 1980).

From this diagram it is evident that to keep clear of the rapidly ascending limb of the curve, the stock should not be allowed to fall below about 4 million tons. This corresponds to an F of about 0.3, which is already higher than in the most productive earlier years of the fishery and about twice the value of M. This stock size is located on the stock-recruitment array for the Norwegian spring spawning herring by the vertical broken line of Fig. 6. The variability of recruitment is such that a rather higher stock size, perhaps in the region of 6 million tons, would be needed to reduce to an acceptable level the risk of another year-class as small as that of 1965 setting in motion the collapse feed-back loop. A proper risk assessment, showing the probability of collapse against stock size, could be made from the observed variability of recruitment using Horwood's (1982) method or by repeated runs on a computer.

The decision-maker then has the unenviable task of weighing various probabilities of collapse against the implications of restraining the fishery to a lower operational level than that at which it would otherwise have been under the influence of the usual short-term incentives. The price to pay for this more prudent exploitation might include a little smaller average yield, although an F in the region of 0.3 is probably close to the mode of the "equilibrium" yield curve for the fishery: such differences as there might be would be lost in the "noise" of fluctuations in R and price elasticity.

More significant is that the somewhat smaller fishery would be operating at a substantially higher mean catch per unit effort than would otherwise have been the case: effective regulatory measures would therefore be needed to ensure that the effort does not gradually creep up to the danger zone.

Fig.7 shows a hypothetical illustration of prudent exploitation in the case of fishery which is liable to "collapse". Figure 7 (a) is the equilibrium yield (effort curve incorporating the stock-recruitment curve of Figure 7 (b). Fig. 7 (c) is the corresponding biomass/effort curve. The depth of shading is an indication of the risk of collapse, i.e. if the fishery is being forced by one or two poor recruitments into the positive feed-back loop illustrated in Fig. 4, as happened in the Norwegian fishery. It would clearly be more "prudent" for the fishery to operate at, say, point B then at the MSY point A; and although the total yield would be smaller, the catch per unit effort would be higher.

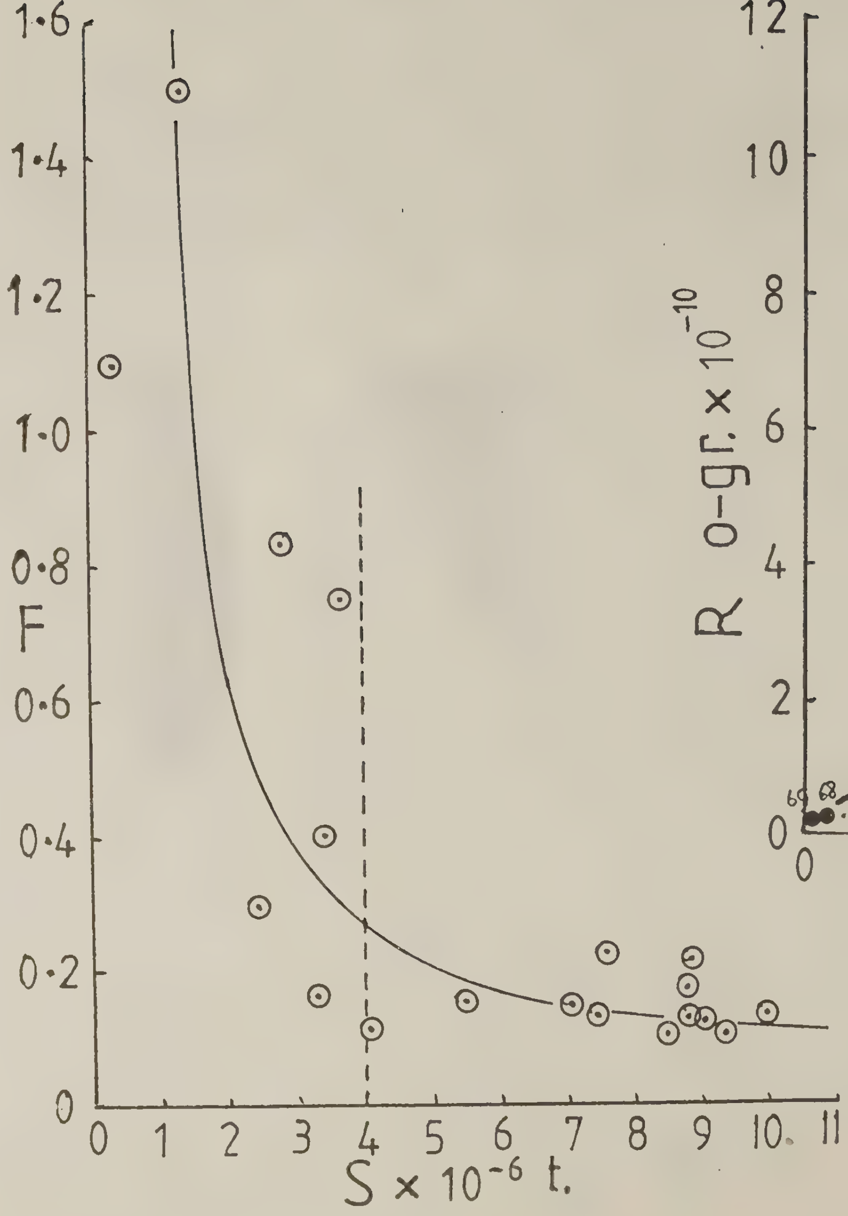
The difficulty for the administrator of introducing such restraints, and for the scientist of convincing him and the fishermen that it is in their longer-term interests to do so, is clearly formidable. At the time, before the collapse, it was virtually impossible (see Saetersdal, 1980). But now, taking a global view, we are sadder but wiser--or should be, if the lesson is put across effectively. Thus, it is significant that although the stocks of both the Norwegian spring spawning herring and the Icelandic summer spawners were reduced to very low levels, fishing was stopped by decree while a stock remnant still remained (Jakobsson, 1980). The same is true for the North Sea herring and the British Columbia herring (Hourston, 1980). All those are showing signs of recovery, albeit slowly in the first three cases. In contrast, fishing continued unrestrained until the bitter end in the Icelandic spring spawning herring fishery and in the California sardine fishery; both these stocks disappeared completely.

I am indebted to Dr. S. Tanaka for telling me that in both the two classic cases of collapse of Japanese fisheries, the Hokkaido herring in the 1930's and the sardine in the late 1940's, fishing intensity remained high on the dwindling stocks until it was no longer worthwhile for the fishermen to put to sea. The Hokkaido herring disappeared and has never recovered; the sardine has recovered but only after a lapse of some 30 years.

The assessment of exploitation risk is an example of the kind of decision that arises in modern fisheries "management", involving both equilibrium and transient states. No doubt many other examples could be cited which are at least or more complex, e.g. those arising if more positive management of multi-species is attempted along the lines

Fig. 5.

Relationship between stock size and fishing mortality coefficient F in the the Norwegian spring spawning herring fishery from 1950 until the collapse of the the fishery in 1971. The vertical broken line shows the stock level at which the rapid escalation of F begins. (Data from Dragesund, Hamre and Ulltang, 1980).



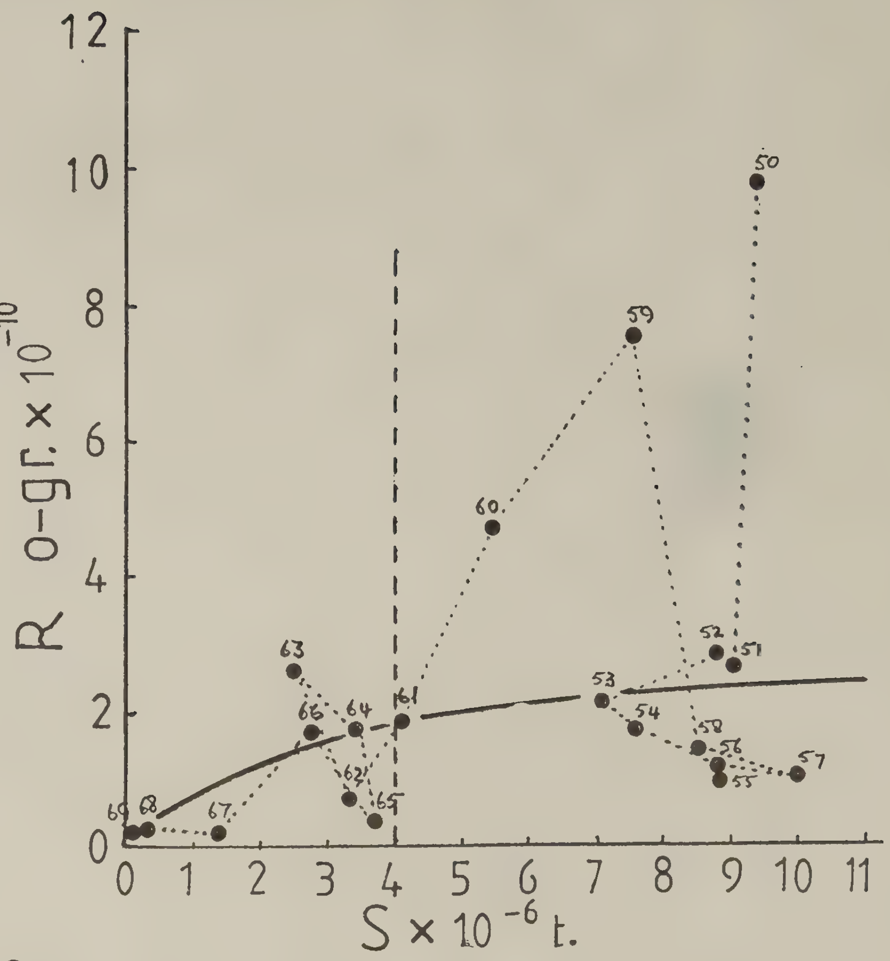


Fig. 6. Stock-recruitment array for the Norwegian spring spawning herring fishery over the same period as Fig.5. The vertical broken line indicates the critical 4 m. tonne stock level of Fig. 5; but to reduce the risk of the fishery becoming unstable through a year class as poor as that of 1965, a stock of some 5 or 6 m tonnes would be required (see text).

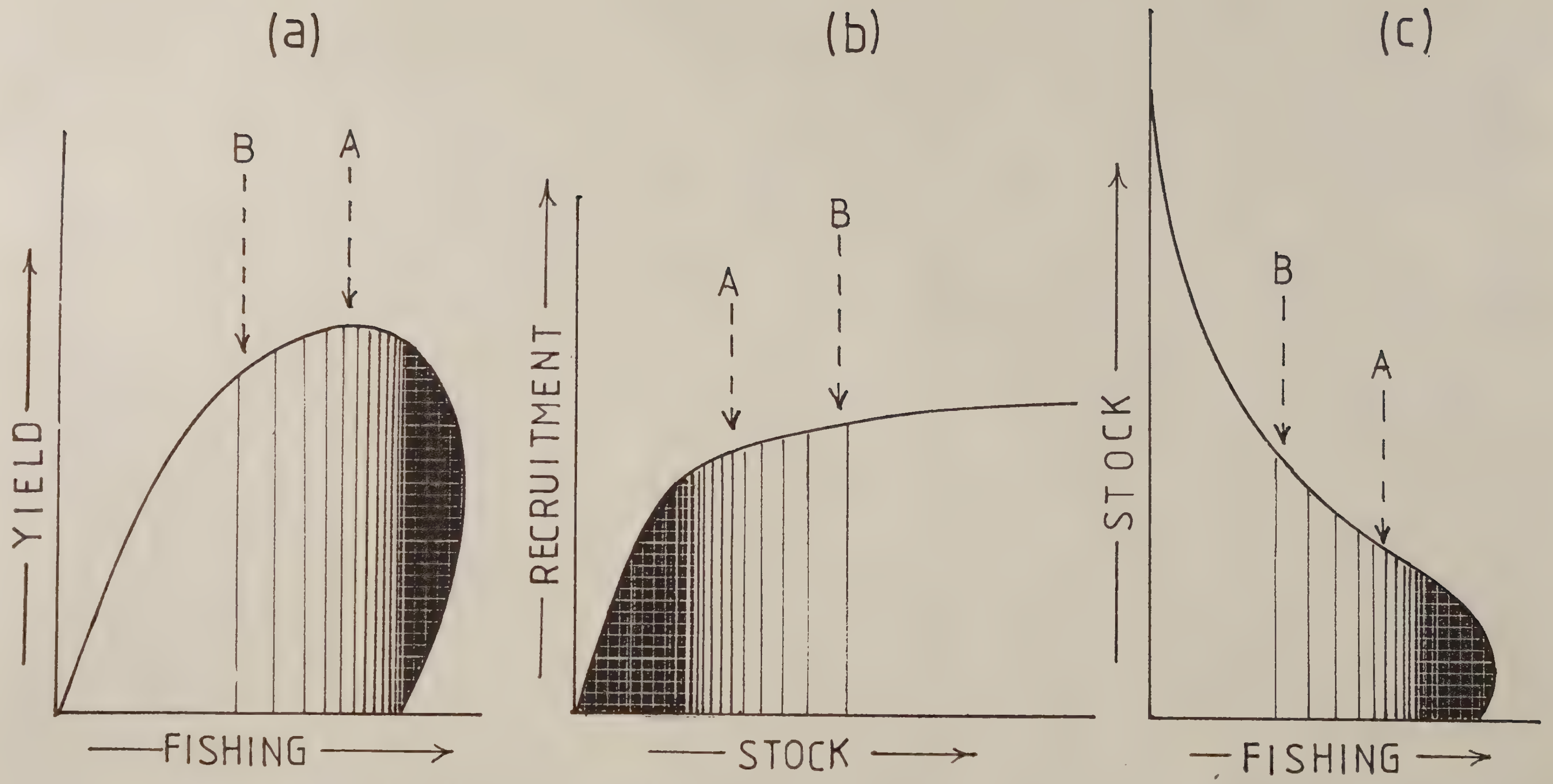


Fig. 7. Hypothetical illustration of the concept of "prudent exploitation" in a fishery with a strong inverse relation between q and density, a weakly-compensated stock-recruitment and a moderate to highly variable recruitment. Prudent exploitation would require the fishery to operate at B of Fig. 7 (a) compared with the maximum equilibrium yield point A. Figs. 7 (b) and (c) show the implications of points A and B on the stock-recruitment and c.p.u.e. curves, respectively, for the fishery in question.

practiced in Canadian and US fisheries. It is pertinent to ask whether the conventional structure of and communication between the scientific and decision-making sides is capable of providing the requisite liaison.

One difficulty at this point is the opacity of the processes at key links in the socio-economic sub-system. How science affects the way decisions are reached in the board rooms of the major fishing companies, or how it affects the attitude of individual owner-skippers with a heavy mortgage to pay on their boat, is not readily available. What happens at the decision-making level in government or in the international fisheries bodies is not necessarily any more visible. The International Council for the Exploration of the Sea (ICES), I am glad to see, still provides first-stage scientific assessments to the European Commission on fisheries within the latter's jurisdiction, which are openly published as Reports of the Advisory Committee on Fishery Management. But what happens thereafter, as the scientific assessment is moved up the hierarchy inside the Commission to the ultimate decision-making by the Council of Ministers, is known to a privileged few only.

This situation might not matter if the scientific basis for decisions were easily and quickly tested against results. It is characteristic of natural resource systems, and highly variable fisheries in particular, that this is not so. A high degree of mutual trust and confidence between the scientists and the decision-makers is called for if fishery collapses of the kind we have witnessed during the last decade are to be avoided. Still more will this be true if we are to move into more positive fishery management such as advocated by Gulland (1980) for the North Sea.

My impression - admittedly vague and with only limited support from hard evidence (but see, e.g. Glantz 1981; and Saetersdal 1980) - is that the decision-makers still take only passing notice, most of the time, of what the scientists have to say. If that is right, perhaps we should be giving some thought as to how to get the message across rather better in the future. It seems to me that one essential step is to acknowledge that the first stage assessment of the fishery is a sophisticated exercise in the application of the scientific method to the analysis and interpretation of complex data from various sources and of uncertain reliability. It requires also a sound understanding of the natural history of the species and of the ecology of the population in question. That being so, there is everything to be gained from publication of those assessments so that they are open to scrutiny by the competent scientific community, just as would be any regular research findings. Not only would this improve the standard of the investigations; it would also give those who have to use them the added confidence that they have run the gauntlet of open scientific peer review, which is the furnace in which the steel of all good scientific research is forged.

REFERENCES

Bakken, E. Recent history of Atlanto-Scandian herring stocks. (This volume).

Beverton, R.J.H. (In press). Resource variability and exploitation strategy. In Segundo Seminario Tailler. Base biologicas para el uso y manejo de recursos naturales renovables. Resursos biologicos marinos (J.C. Castilla, ed.). Monografias Biologicas (2).

Beverton, R.J.H. and A.J. Lee. 1965. Hydrographic fluctuations in the North Atlantic Ocean and some biological consequences. Inst.Biol.Symp. No.14, pp. 79-107. In Biological significance of climatic changes in Britain (E.C. Johnson and L.P. Smith, eds). Academic Press, London.

Butterworth, D.S. Assessment and management of pelagic stocks in the Southern Benguela system. (This volume).

Caddy, J.F. 1983. An alternative to equilibrium theory for management of fisheries. Presented at Expert Consultation on the Regulation of Fishing Effort (Fishing Mortality). 17-26 January 1983, Rome.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:307-313.

Dragesund, O., Hamre, J. and Ø. Ulltang. 1980. Biology and population dynamics of the Norwegian spring spawning herring. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:43-71.

Garrod, D.J. 1982. Stock and recruitment - again. Fish.Res.Tech.Rep. 68, MAFF, Lowestoft.

Glantz, M.H. 1981. Considerations of the societal value of an El Niño forecast. pp. 449-476. In Resources Management and Environmental Uncertainty: lesson from coastal upwelling fisheries. Wiley and Sons, New York.

Gulland, J.G. 1980. Long-term potential effects from management of the fish resources of the North Atlantic. J.Cons.int.Explor.Mer. 40(1):8-16.

Holt, S.J. 1980. Sharing our planet with wildlife. J.Fauna Pres.Soc. XV(3):259-261.

Horwood, J.W. 1982. The variance of population and yield from an age-structured stock, with application to the North Sea herring. J.Cons.int.Explor.Mer. 40(3):237-244.

Hourston, A.S. 1980. The decline and recovery of Canada's Pacific herring stocks. Rapp.P-v.Réun.Cons.int.Explor.Mer 177:143-153.

Jakobsson, J. 1980. Exploitation of the Icelandic spring and summer spawning herring in relation to fisheries management, 1947-1977. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:23-42..

Kawasaki, T. Why do some pelagic fishes have wide fluctuations in their numbers? - biological basis of fluctuation from the viewpoint of evolutionary ecology. (This volume)

Kondo, K. 1980. The recovery of the Japanese sardine - the biological basis of stock-size fluctuations. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:332-354.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. Trans.Amer.Fish.Soc. 106(1):1-11.

MacCall, A.D. 1976. Density dependence of catchability coefficient in the California Pacific sardine, Sardinops sagax caerulea, purse seine fishery. Calif.Coop.Ocean.Fish.Invest.Rep. 18:136-148.

Pope, J.G. 1980. Some consequences for fisheries management of aspects of the behaviour of pelagic fish. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:466-476.

Saetersdal, G. 1980. A review of past management of some pelagic stocks and its effectiveness. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:505-512.

Saville, A. and R.S. Bailey. 1980. The assessment and management of the herring stocks in the North Sea and to the west of Scotland. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:112-142.

Sharp, G.D., J. Csirke and S. Garcia. Modelling fisheries: what was the question? (This volume).

Ulltang, Ø. 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:489-504.

Ursin, E. 1982. Stability and variability in the marine ecosystem. Dana. (2):51-68.

PART IV - APPLICATION OF METHODS AND THEORY

PARTE IV - APLICATION DE METODOS Y TEORIA

VERTICAL DISTRIBUTION OF LARVAE OF MACKEREL *Scomber scombrus* AND MICROPLANKTON, WITH SOME CONCLUSIONS ON FEEDING CONDITIONS AND SURVEY METHODS

by

S.H. Coombs, J.A. Lindley and C.A. Fosh

Natural Environment Research Council (NERC)
Institute for Marine Environmental Research
Prospect Place, The Hoe
Plymouth, Devon PL1 3AX
United Kingdom

Resumen

El muestreo con registrador continuo de plancton (RCP) ha sido utilizado en el Mar del Norte y el Atlantico Norte para describir las variaciones a largo plazo en la distribución, abundancia y ocurrencia estacional del plancton, incluyendo huevos y larvas de peces. Estos resultados han formado la base de un estudio de la disponibilidad de alimento durante la fase larvaria y la influencia de las variables ambientales.

Al igual que en otros estudios empíricos de correlación entre índices de stocks adultos y plancton no se encontró ninguna relación consistente. En forma superficial, estos resultados proporcionaron evidencia para rechazar la hipótesis convencional de que el reclutamiento es controlado por la disponibilidad de alimentos. Por otro lado, la abundancia de organismos alimenticios en el mar raramente ha sido medido en concentraciones que sean adecuadas para la sobrevivencia de larvas de peces. Sin embargo, los estimados comúnes de la abundancia de plancton están basados en un muestreo que integra una escala demasiado amplia en sentido horizontal y vertical que resulta inapropiado en relación al ambiente que puede ser percibido por una larva; por lo tanto, un muestreo a una escala de resolución más fina puede reflejar la verdadera concentración y disponibilidad de alimento para las larvas.

El muestreo vertical estratificado del plancton ha mostrado la agregación de larvas de caballa (*Scomber scombrus*) en capas estrechas a la misma profundidad en que ocurre la máxima productividad primaria potencial (indicada por la concentración de clorofila - a) y el microplancton del rango de tamaños 102-161 um. es abundante. Este rango de tamaños está constituido de nauplias de copépodos y estadios copépodiformes, los que también constituyen los items principales en el contenido intestinal de las larvas.

La concentración de microplancton de tamaño adecuado para la alimentación alcanzó al menos 200 partículas 1^{-1}, lo que probablemente es suficiente para la sobrevivencia de las larvas.

Estos hallazgos parecen indicar que si se quieren evaluar las condiciones de alimentación favorables para la sobrevivencia de las larvas, es necesario muestreos de plancton a una escala más fina en un área geográfica suficientemente amplia del área de desove. Un método de conciliar los problemas logísticos de muestreos en estas escalas tan extremas es usando un muestrador de perfil batimétrico de alta velocidad tal como el Registrador Oceanográfico Ondulante (ROO) o el "Batfish", para identificar áreas con condiciones potencialmente favorables, y después concentrar el muestreo de plancton de pequeña escala en estas áreas. Una ventaja adicional del muestreo continuado de plancton a alta velocidad es que, a diferencia de lo que ocurre con el muestreo convencional, con la integración del muestreo a través del área muestrada se reduce el sesgo que resulta de tratar una sola estación como representativa de un área más amplia, y se reduce la varianza generada por la distribución desigual del plancton. Por ejemplo, de esta forma los reconocimientos cuantitativos de huevos de peces, y por lo tanto la estimación del tamaño del stock desovante, se pueden llevar a cabo a alta velocidad, colectando una cantidad relativamente pequeña de material y se pueden obtener estimados de la abundancia de la población que son mejores que los obtenidos por métodos convencionales.

INTRODUCTION

Conventional theories of fluctuation in year-class strengths of marine fish stocks have stressed the importance of availability of food, particularly the concept of the "critical period" for first-feeding larvae (see May, 1974). However, empirical studies, based on conventional sampling at the kilometre scale, have generally failed to show a relationship between the abundance of planktonic food and year-to-year changes in recruitment (for example, see Gulland, 1965). Similarly, investigations of the interrelationships between indices of adult fish stocks, environmental variables and broad-scale estimates of plankton abundance derived from sampling at a scale of tens of kilometres with Continuous Plankton Recorders (see Edinburgh, Oceanographic Laboratory, 1973) have also failed to show any clear causal links (Garrod and Colebrook, 1978; unpublished results). Superficially, and within the limitations of the methods of data collection, these results might seem to give grounds for rejecting the hypothesis of dependence of recruitment on the availability of food. Moreover, concentrations of food particles at the levels needed for successful rearing of larvae have rarely been observed in the sea. Laboratory studies have indicated a typical requirement of first-feeding larvae for prey concentrations of 100-1000 particles l^{-1} (e.g. O'Connell and Raymond, 1970; Laurence, 1974 and 1977); a few reports have described larval feeding at food concentrations of 10-100 particles l^{-1}, but this is usually accompanied by significantly depressed rates of growth and survival (e.g. Houde, 1978; Werner and Blaxter, 1980). By contrast, in the sea, suitable food organisms have rarely been reported at concentrations exceeding 20 particles l^{-1} (e.g. Arthur, 1977; Beers and Stewart, 1969).

It may well be, however, that food abundance has been measured by sampling at an inappropriate scale. Recently, a few reports of stratified vertical sampling have revealed layers of particle concentration exceeding 100 particles l^{-1} and in some cases there was evidence that larvae were aggregating on the food concentrations (Lasker, 1975; Ellertsen et al., 1977; Owen, 1981). Clearly, the ability to detect patches of adequate food concentration is dependent on sampling with an appropriate spatial discrimination; furthermore, because gradients of variability in the sea are greater vertically than horizontally (for example, see Steele, 1978) the critical plane for sample resolution is the vertical, and discrimination should be on a scale of metres, or less, to match the searching potential of a fish larva. It seems reasonable to assume that ontogenetic and diel vertical migrations of fish larvae would provide a feasible mechanism for encountering layers of aggregated food particles which would be available only over inaccessible horizontal distances.

It follows from these assumptions that, in order to measure plankton abundance as an estimate of available food for fish larvae, it is necessary to sample discrete depth layers instead of using large-scale integrated sampling.

In the present paper results are presented from vertically stratified plankton sampling designed to explore the relationship between the vertical distribution of mackerel larvae *Scomber scombrus* and microplankton. The implications of the results are discussed in relation to the design of plankton sampling for investigations of the dependence of recruitment on plankton abundance, and suitable methodologies are outlined. Additionally, experience from the use of high-speed and broad-scale sampling techniques is used to suggest improved sampling strategies for ichthyoplankton surveys, as required, for example, to provide data for stock management.

MATERIAL AND METHODS

Vertical distributions of fish eggs and larvae were investigated by oblique hauls at selected stations (Fig. 1) in 1974, 1975, 1978, 1980 and 1981 using a modified Longhurst-Hardy Plankton Recorder (LHPR; Longhurst and Williams, 1976) towed at a speed of 2.3 knots. This instrument takes discrete samples of plankton from a recorded volume of water over a known depth range while measuring temperature continuously. For these studies the filtration system consisted of a conical nylon net of mesh aperture 280um or 710um (for egg sampling only) with a flowmeter at the mouth and a unit containing two rolls of gauze (mesh aperture 280um) which were advanced so that discrete samples of plankton were taken at pre-determined intervals of 30, 60 or 120 seconds. On completion of a haul the rolls of gauze containing the plankton samples, were placed in 3% or 4% formaldehyde solution and subsequently analysed for fish eggs and larvae. These data were processed with the depth and flow information to give a numerical estimate of abundance over successive standard depth intervals.

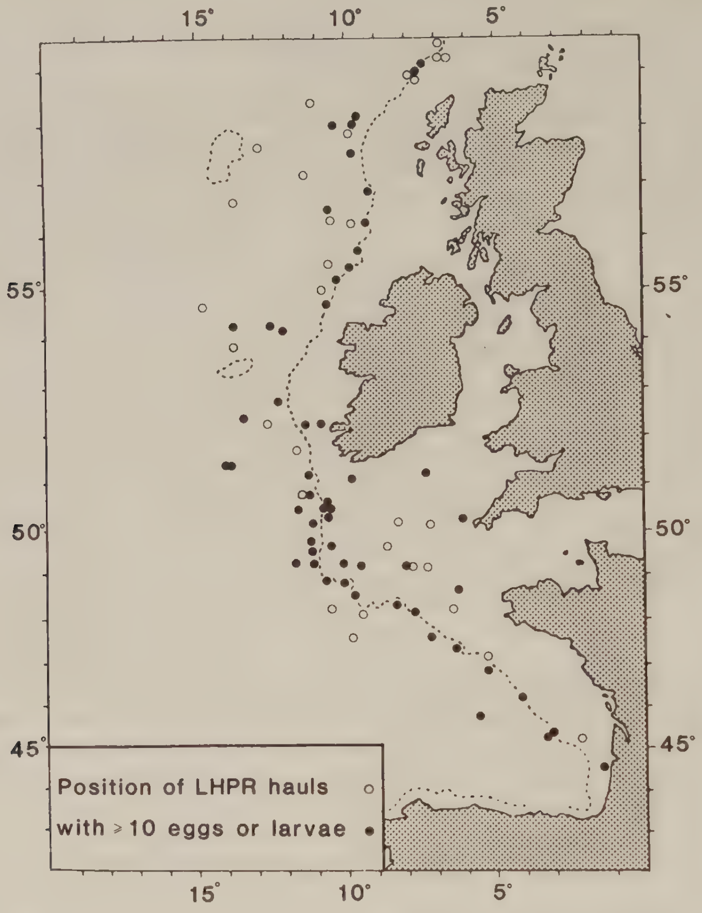


Fig. 1. Positions of LHPR hauls taken to the west of the British Isles in the years 1974-1981.

The vertical distribution of microplankton was investigated in May and June 1980 (Table 1) using an LHPR system equipped with a fine-mesh net in addition to the coarse net described above; a fine polyester gauze (53um mesh) was used for the filtering net as well as the sampling rolls in the cod-end unit (for a full description see Williams *et al.*, in press). This "fine mesh" system was mounted on the sampler frame above the "coarse mesh" system (280um or 710um) so that both intake apertures were in line and separated by 45cm at their centres. Microplankton samples were preserved in 3% formaldehyde from which they were subsequently transferred to 1% solution for analysis by a Coulter Counter size frequency analyser, the results being expressed as equivalent spherical diameter of the particles; control samples and those selected for species analysis were examined by inverted light microscope for identification and measurement of specimens. On selected LHPR hauls in May and June 1980 (Table 1), chlorophyll-*a* was measured at intervals of 15 seconds by a sensor (Aiken, 1981a) attached to the sampler frame.

Table 1 Tows with double-net version of the LHPR for mackerel larvae (coarse mesh), microplankton (fine mesh) and concurrent measurements of chlorophyll-*a*.

Date 1980	Time GMT	Sample validity: valid + or invalid - Coarse mesh	Fine mesh	Chlorophyll	No. of mackerel larvae
1 May	1632	+	-	-	0
2	2229	+	+	-	111
4	0213	+	+	-	260
7	2312	+	-	+	16
9	1114	+	+	-	0
10	1930	+	+	+	0
14	1113	+	+	+	162
16	2251	+	+	+	27
17	0402	+	+	+	91
17	0925	+	+	+	55
17	1536	-	+	+	-
2 June	0906	+	+	-	62
3	1728	+	+	+	0
4	1422	+	+	+	0
7	1801	-	-	+	-
8	2031	+	+	+	35
9	1855	+	-	+	9
11	1625	+	+	+	237
14	1007	-	-	-	-

The geographical distributions of eggs and environmental variables were investigated by sampling with the Undulating Oceanographic Recorder (Aiken, 1981b) along two transects (Fig. 2) in the Celtic Sea in May 1981 (see Coombs *et al.*, 1981b). The UOR is an instrument-carrying body which undulates vertically along a pre-set path when towed at normal cruising speeds behind the survey vessel. Inside the UOR is a data logging system which scans sensors for depth, temperature, chlorophyll-*a* and salinity at intervals of 15 seconds, thus providing vertical profiles of these variables along the towing track. The UOR also contained a simple plankton sampler consisting of a single net bag (710um mesh aperture) with integral digital flowmeter; this provided a single sample on each deployment of the UOR, representing about 0.7m^3 of water filtered per kilometre of the tow. These samples were preserved in 3% formaldehyde solution and subsequently analysed for fish eggs.

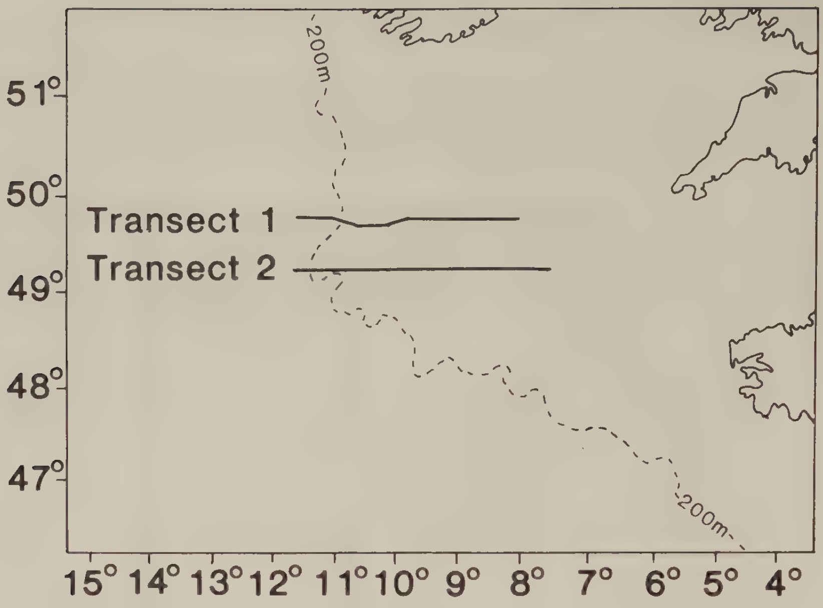


Fig. 2. Tracks along which the Undulating Oceanographic Recorder was towed in May 1981.

RESULTS

Vertical Distribution of Mackerel Eggs and Larvae

As was found previously in the Celtic Sea (Coombs et al., 1981a), mackerel eggs were taken from the surface to depths of several hundred metres in the early part of the spawning season, in March and April; later in the season, in May and June when the seasonal thermocline was established, the eggs were mostly in the upper mixed layer above about 60 m depth (see Fig. 3 and, for detailed examples, Fig. 4). The majority of larvae were taken at shallow depths (<60m) in all months sampled (March to June), although before May they were present in only a few hauls (see Figs. 3, 4 and 5). More significantly for the present investigations, larvae were concentrated within a narrower depth range (10-20 m in vertical extent) than the eggs (Table 2 and see Figs. 4 and 5). There was no consistent difference between the vertical distributions of different size categories of larvae (Fig. 5), (but post-larvae at about 18mm in length, i.e., larger than the larvae in our study, have been reported by Nellen and Hempel, 1970, as being abundant in the neuston). Highest numbers of larvae were sometimes taken at the surface but the maximum was more often in sub-surface waters in the depth range of 20-40 m (Fig. 5). As in previous studies of the smaller sizes of mackerel larvae (Grave, 1978; Southward and Bary, 1980), there was no diel change in their depth of occurrence in the present study.

Table 2 Index of vertical dispersion for mackerel eggs and larvae taken to the west of the Bristish Isles.

	Interquartile range, metres			
	March	April	May	June
Eggs, all stages	92	105	41	30
Larvae, 0-3.9 mm	-	39	21	24
" , 4.0-5.9 mm	-	25	23	21
" , 6.0-7.9 mm	-	18	28	25

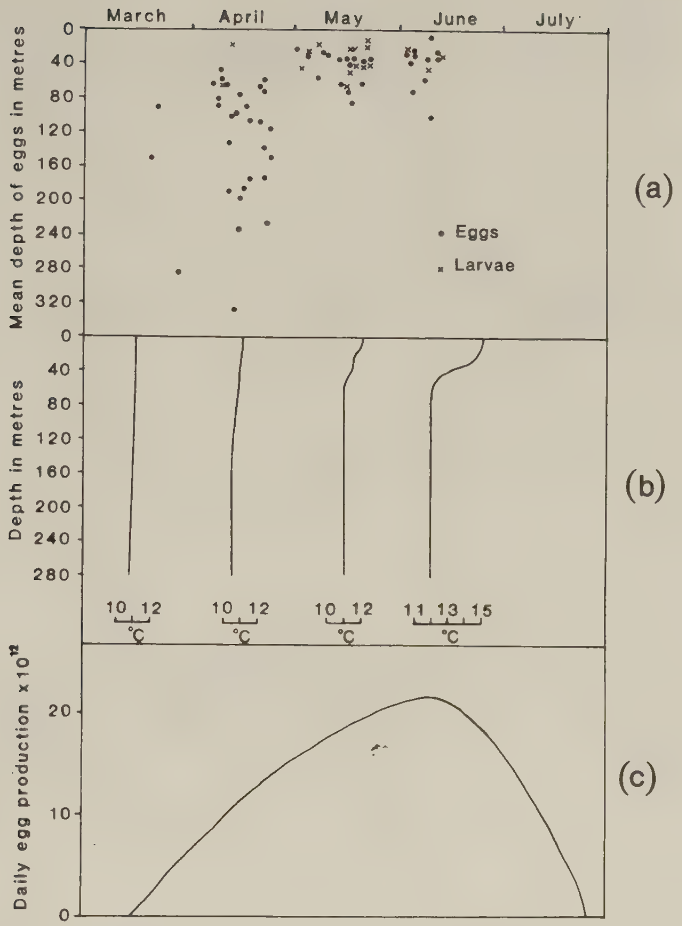


Fig. 3. (a) The mean depth of mackerel eggs (all stages of development) and mackerel larvae (<8.0mm in length) on individual LHPR hauls on which>10 eggs or > 5 larvae were taken; (b) representative temperature profiles from the LHPR hauls in each month; (c) egg production curve for the western mackerel spawning stock (based on Lockwood _et al_., 1981).

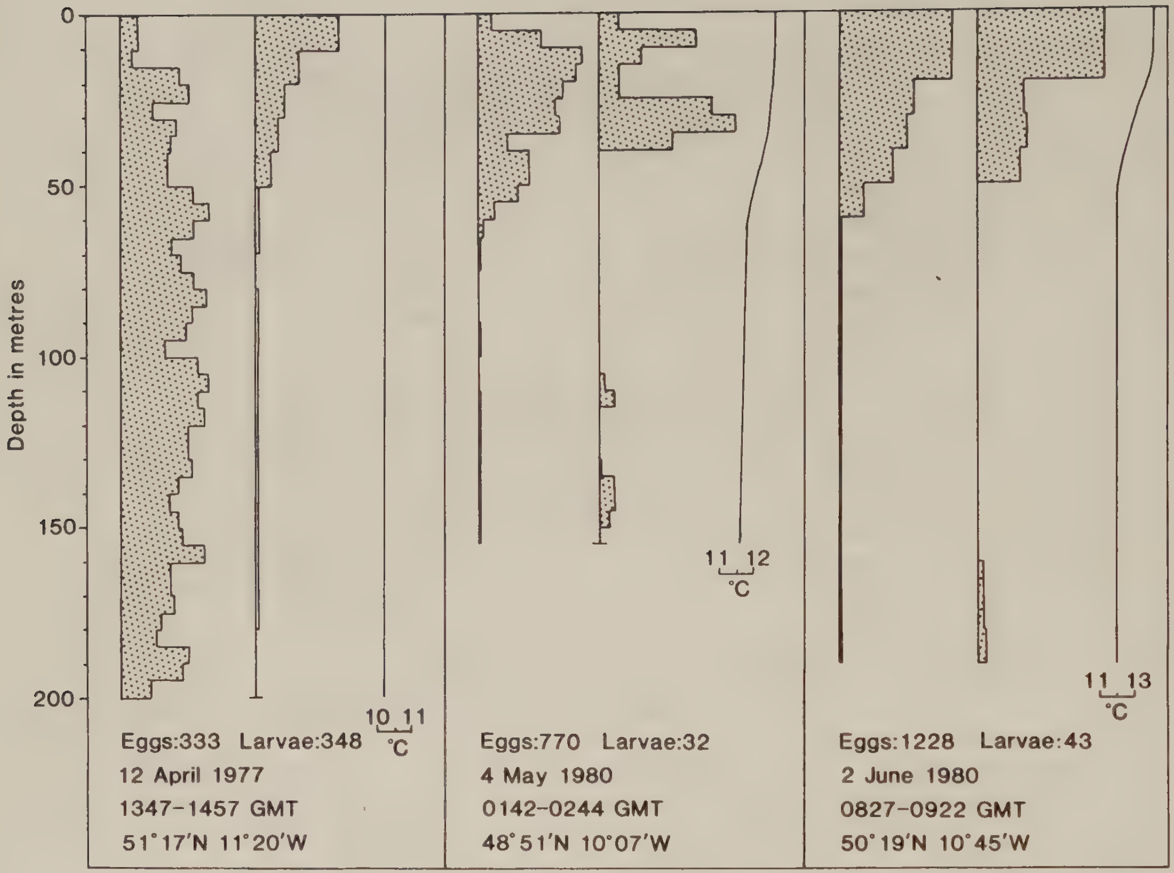


Fig. 4. Representative vertical distributions of mackerel eggs (all stages of development) and larvae (<4.0mm in length) for April, May and June taken on three individual LHPR hauls; the distributions are plotted in units of relative abundance against depth and below each profile are indicated the numbers of specimens on which it was based and station information; alongside the distributions are shown the concurrent temperature profiles.

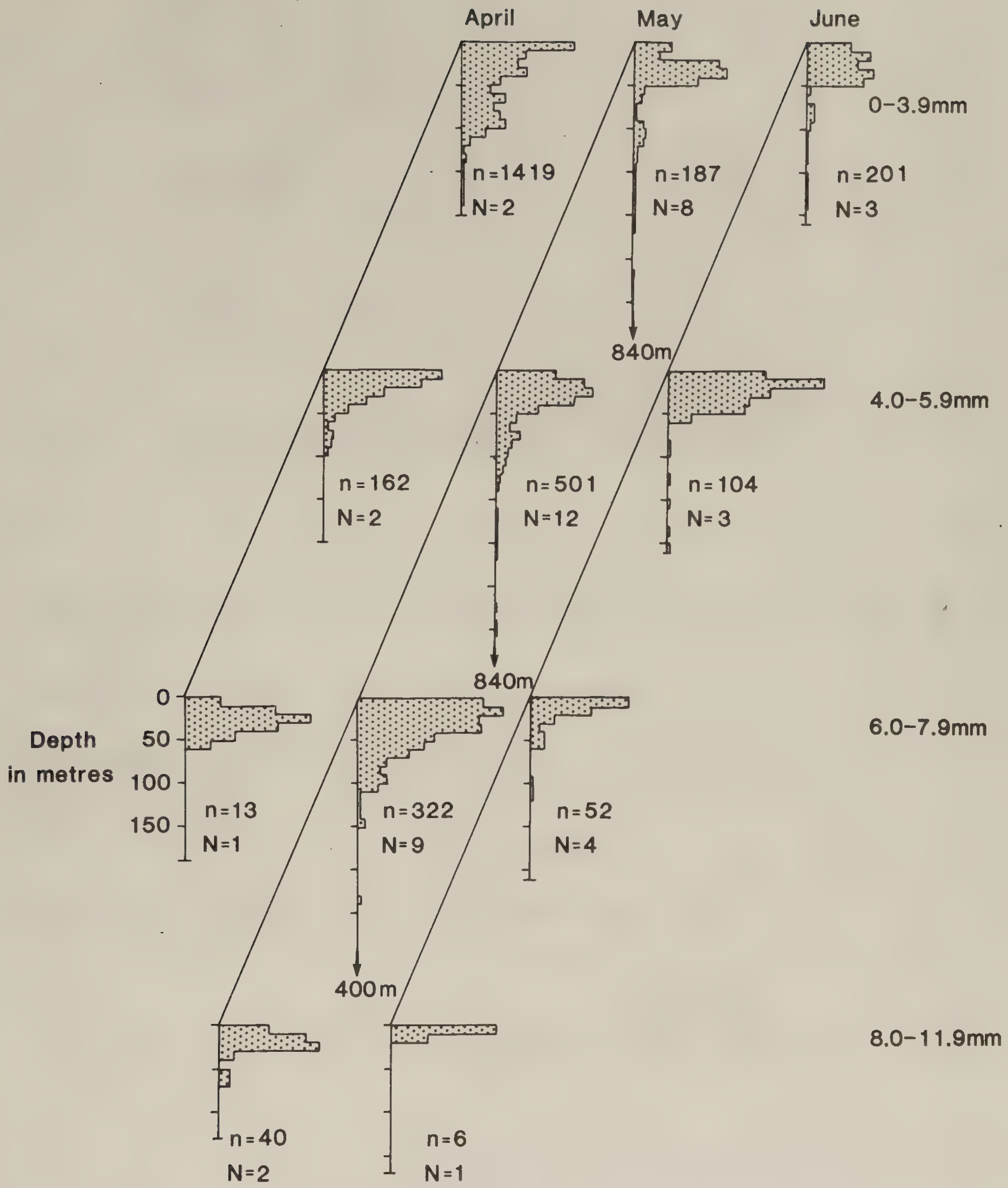


Fig. 5. Vertical distributions of mackerel larvae in four length groups plotted as the mean distribution from LHPR hauls taken in all years in the months of April, May and June. Each distribution is plotted in units of relative abundance against depth; alongside each profile are indicated the numbers of larvae (n) and of hauls (N) on which each distribution is based. Only those hauls containing >5 larvae are included.

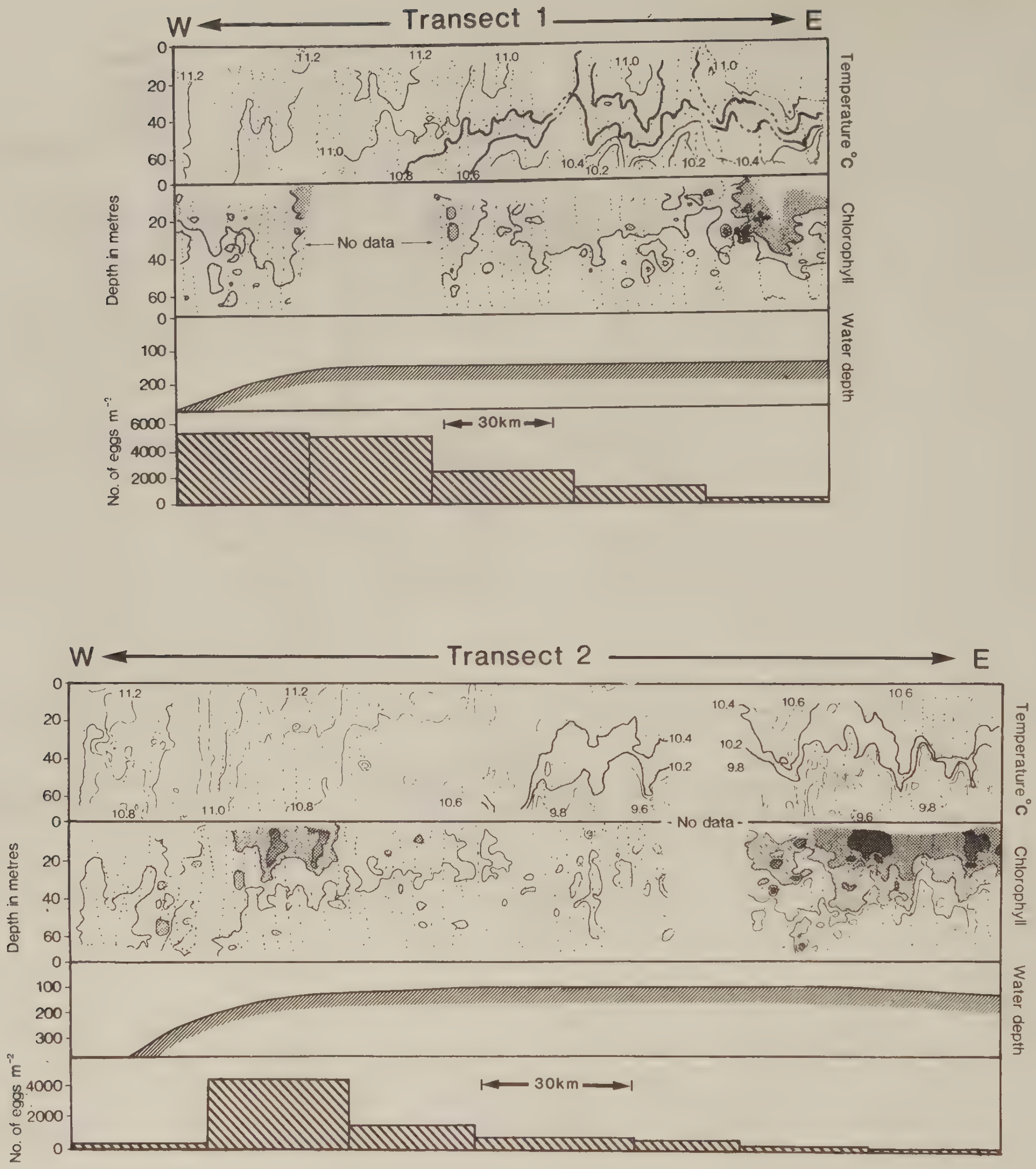


Fig. 6. Temperature and chlorophyll-a sections taken by UOR sampling along two transects in the Celtic Sea (see Fig. 2); also indicated are the water depth and numbers of early development stage mackerel eggs taken concurrently along sections of each transect. Temperature is contoured at intervals of 0.2°C with selected isotherms drawn more heavily to show the structure more clearly. Chlorophyll-a concentration is contoured at intervals of 1.0mg m^{-3}. and stippled at progressively darker shades above 1.0mg m^{-3}. The small dots indicate positions of each data measurement made along the tow.

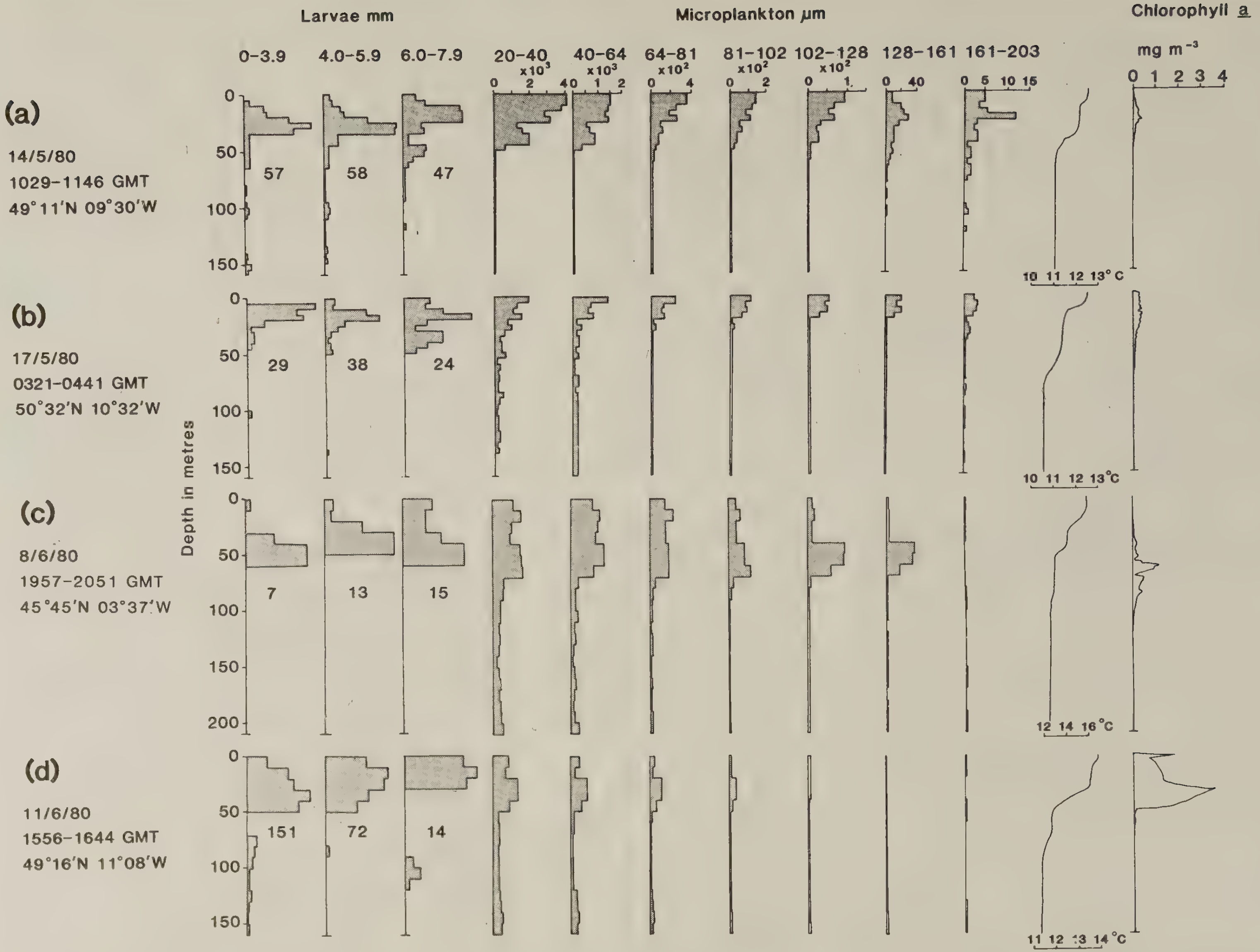


Fig. 7. The vertical distributions of mackerel larvae and microplankton and the concurrent temperature and chlorophyll-a profiles taken on four selected LHPR hauls. The distributions of larvae are plotted in units of relative abundance against depth; below each profile is indicated the number of larvae on which the distribution is based. The distributions of microplankton are plotted as numbers of particles l^{-1} in each size category. Sampling resolution was at a vertical scale of 5m for the hauls taken in May (a and b) and 10m for the hauls in June (c and d).

Distribution of Mackerel Eggs and Larvae in relation to Temperature, Chlorophyll-a concentration and Microplankton abundance

Dickson et al., (1980), have drawn attention to the similarity between the location of mackerel spawning grounds at the shelf-edge to the west of the British Isles and a corresponding area of upwelling and associated high potential productivity (see, also, Pingree and Mardell, 1981). The general favourability of the area for spawning was shown more precisely by the relationship between abundance of mackerel eggs and concurrent measurements of chlorophyll-a (as an index of potential productivity) taken by UOR sampling along two transects in the Celtic Sea in May 1981 (Fig. 2). Highest numbers of mackerel eggs were taken at the western ends of both transects in relatively unstratified water at the shelf-edge (Fig. 6); further to the east egg numbers were lower and thermal stratification was increasingly evident at 30-50m depth in a pattern resembling internal waves which are characteristic features of the area (Pingree and Mardell, 1981). Associated with the stratified water at the eastern ends of the transects were rich concentrations of chlorophyll-a in the overlying layer of warmer water. Further to the west chlorophyll-a was generally low, but there was distinct evidence on Transect 2 and (less distinctly because of a gap in sampling) on Transect 1 of a region of enhanced values near the shelf-edge corresponding with the region of peak numbers of mackerel eggs (Fig. 6). Information about the distribution of chlorophyll-a provides an indication of potential primary production but its value as an indicator of availability of food for fish larvae depends on the relationship between chlorophyll-a and the microplankton which forms their immediate food source.

Results from sampling for microplankton in the size range 20-203um at the mackerel spawning rounds in May and June 1980 (Table 1) showed that plankton in this size range was relatively abundant in warm surface water and intermediate layers of the thermocline from about 50m to the surface (for examples, see Fig. 7). Below the thermocline microplankton was much less abundant, particularly so in the case of the smaller size categories. Highest concentrations were often in the most superficial 20m depth range but on several hauls prominent concentrations, most noticeably of the larger size groups, were observed somewhat deeper, often within the temperature discontinuity (for examples, see Fig. 7). In one haul, when there was little temperature stratification, microplankton was more evenly distributed to a depth of several hundred metres (Fig. 8), although the highest concentrations were all within the upper 150 m.

Profiles of chlorophyll-a taken concurrently with microplankton sampling showed detectable concentrations only within the upper 60m depth range, corresponding approximately with the thickness of the upper mixed layer above the thermocline (for examples, see Fig. 7; see, also, Fig. 6). Low values (0.5mg m^{-3}) were recorded on most hauls; only twice, both in June, were concentrations encountered which exceeded levels of 1.0mg m^{-3} (Figs. 7c and d). As other workers have found (e.g. Longhurst, 1976; Holligan and Harbour, 1977), the highest values of chlorophyll-a were found at intermediate depths below the surface, frequently in association with the thermocline (e.g. Fig. 7d), although this was not a feature of the chlorophyll distributions obtained by UOR sampling (Fig. 6). On several hauls concentrations of chlorophyll-a corresponded with higher counts of phytoplankton and peaks in the abundance of microplankton particles below 102um in size (e.g. Fig. 7d). In general, while the concentrations of chlorophyll-a reflected the generally increased abundance of microplankton in the upper 60m of water depth, there was little precise correspondence with individual layers of microplankton.

Composition of the microplankton taken in the oblique hauls with the LHPR was typical of fine mesh plankton samples from around the British Isles in the spring. The most common organisms in the size range 100-203um* were nauplii and copepodites of *Oncaea* spp. and *Oithona* spp. and nauplii of *Paracalanus parvus* and *Pseudocalanus minutus*; less numerous were copepodite stages of *P. parvus*, *P. minutus*, *Acartia* spp. and *Microsetella* spp. Below 100um in size, phytoplankton was an important component being mostly *Rhizosolenia* spp., *Coscinodiscus* spp., *Peridinium* spp., *Ceratium* spp. and *Thalassiosira* spp. Larvacea,

---

* Size range is given as the equivalent spherical diameter of the volume of each organism calculated from simple measurements of body dimension and formulae for the volume of similar simple geometric shapes e.g. assuming a cylindrical body form for a copepodite stage of *Oncaea* spp. having a metasome length of 240um and depth of 100um gives an equivalent spherical diameter of 153um.

Foraminifera, Tintinnida and Echinodermata larvae were occasionally present. In the smallest size categories (20-64um), unidentified detritus composed of broken remains, such as detached setae, was recorded in significant amounts.

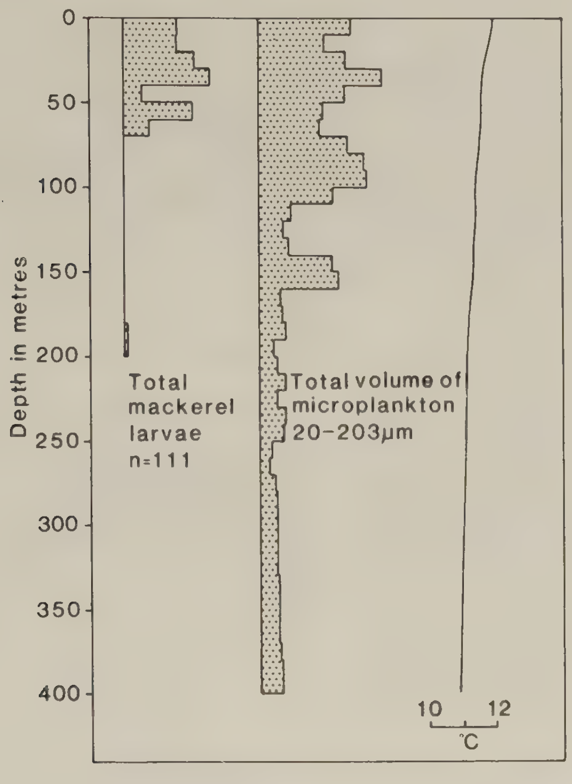


Fig. 8. The results from a single LHPR haul on 2 May 1980 when there was little or no temperature stratification. The distributions of mackerel larvae and microplankton are plotted in units of relative abundance against depth. Below the profile for mackerel larvae is indicated the number of specimens (n) on which the distribution is based.

Comparison of vertical distributions of mackerel larvae and microplankton was complicated by varying levels of abundance between hauls and by the different shapes of individual profiles. In order to derive a quantitative assessment of affinity between the various depth profiles within a haul, similarity measures were calculated between each size group of larvae and microplankton. The method adopted was first a standardization of the depth profiles to give percentage abundance of each larval or microplankton group in each depth interval, followed by calculation of Bray-Curtis similarity coefficients (e.g. Field et al., 1982) between each larval and microplankton group. For each of the three larval size categories, the corresponding similarity coefficients were ranked (i.e. assigned the numbers 1 to 7 according to increasing degree of similarity between the larval profile and the seven size categories of microplankton). This procedure was repeated for all hauls and the agreement between hauls tested using Kendall's "coefficient of concordance" (Kendall, 1955). Significance for this test implies that the relation between the particular larval size category and the various microplankton groups is replicated over several hauls in a way that cannot be due to change permutations. For each larval group, summation of the sets of ranks across all hauls, followed by standard normalization of these totals, allows a visual assessment of the relationships between mackerel larvae and microplankton size groups, as plotted in Figure 9. There was a clear pattern showing a positive relationship, significant at just below the 5% level, between larvae and microplankton of 102-128um and 128-161um in size. The distribution of the smallest larvae, at<4.0mm in length, was most closely related to the smaller of these two size categories of microplankton (102-128um) whereas the relationship was reversed for the two larger size groups of larvae (4.0-5.9mm and 6.0-7.9mm) which were more closely associated with microplankton of 128-161um (Fig. 9).

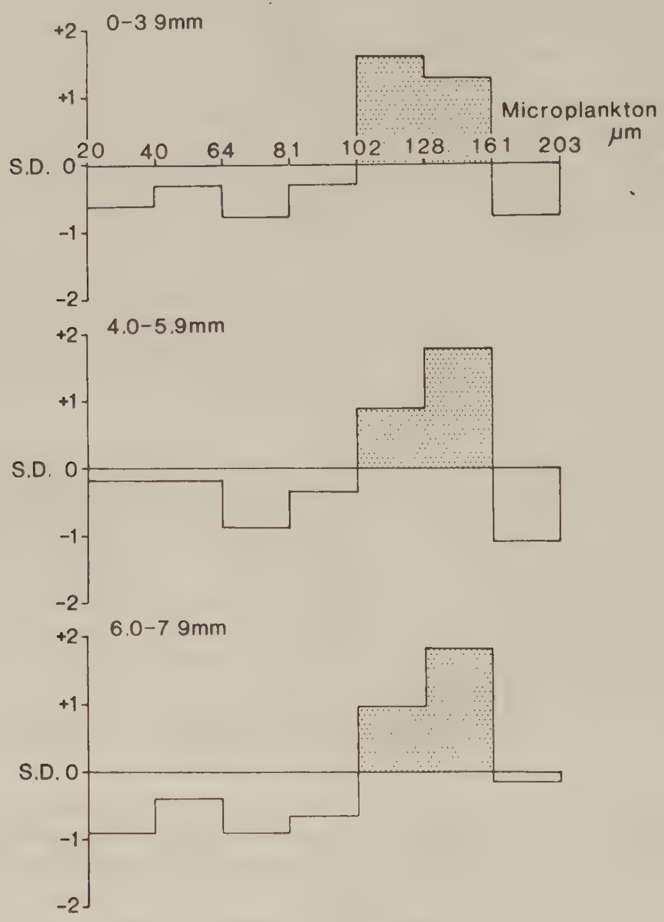


Fig. 9. The relationships between three size groups of mackerel larvae and various size groups of microplankton; for further details see text.

While this method of comparison provides a convenient summary of results from all hauls, it gives little information about the qualitative similarity between individual larval and microplankton profiles; for this purpose vertical distributions are presented from four representative hauls taken in May and June 1980 (Fig. 7). On three of these hauls, microplankton was relatively abundant (Figs. 7a, b and c), whereas on the other haul (Fig. 7d) it was present at a low concentration, particularly in the larger size categories.

On the haul taken on 14 May (Fig. 7a) the majority of larvae were in the upper 50m of the water column where microplankton was generally most abundant; more specifically, the two smaller categories of larvae of 0-3.9mm and 4.0-5.9mm in length were concentrated at 20-25m depth where microplankton of 128-161um and 161-203um in size was most abundant. Similarly on 8 June (Fig. 7c) mackerel larvae were most numerous at 40-60m depth corresponding to concentrations of microplankton, in particular those of 102-128um and 128-161um in size. On both of these hauls (Figs. 7a and c) there were also peaks of chlorophyll-a at the same depth as the larvae. Concentration of particles in the size ranges 102-128um and 128-161um reached maxima of 99 and 39 particles l^{-1} respectively on the haul of 8 June

(Fig. 7c). There was a less precise relationship between the distributions of larvae and individual microplankton profiles for the hauls taken on 17 May (Fig. 7b) and on 11 June (Fig. 7d). Also on 17 May, chlorophyll-a concentration was relatively constant throughout the upper 40m depth range and was not related in detail to the larval distributions. In contrast, on 11 June, when the larger size categories of microplankton were relatively scarce, larvae were abundant at about 40m depth where high concentrations of the smaller sizes of microplankton and chlorophyll-a were also recorded (Fig. 7d).

From the set of double-net LHPR hauls, there appears to have been a good correspondence between the distributions of mackerel larvae and microplankton and a more general similarity with temperature and chlorophyll-a, rather than a detailed coincidence in depth. These relationships reflect the occurrence of peak concentrations of larvae and microplankton in the upper 60m of the water column where the profiles for chlorophyll-a and temperature were most variable. Temperature was more clearly related to the distributions of larvae and microplankton than was chlorophyll-a; however, because of the variability within individual temperature profiles, with one or more secondary thermoclines (see Fig. 7), there was an increased probability of some apparent relationships between temperature and the other profiles.

DISCUSSION

Evidence for a functional relationship between the distribution of larvae and microplankton depends not only on their co-occurrence but also on the suitability of the microplankton as a food source, its concentration in adequate amounts and, ultimately, on agreement between gut contents of larvae and the available microplankton. In the present study, the larvae were associated with microplankton in the size range of 102-161um (see Figs. 7 and 9) which consisted mainly of copepod nauplii and copepodite stages; these are known to be typical components of the diet of mackerel larvae of $<$6.0mm in length and are appropriate in size to the jaw gape of the larvae (Last, 1980). Some preliminary analysis of gut contents of mackerel larvae taken in this study has shown that copepodite stages of *Oncaea* spp. are important dietary items; they were also one of the most numerous organism in the microplankton of 102-161um taken at the same depth as the larvae.

Small larvae ($<$4.0mm in length) were associated with particles of 102-128um in size and larger larvae (4.0-5.9mm) with particles of 128-161um but there was no further increase in the size of particles preferred by the largest larvae (6.0-7.9mm, see Fig. 9). In part this may be the result of the relative scarcity of particles$>$161um (for example, see Fig. 7) and a selective shift of feeding to particles of less than the maximum acceptable size under such conditions (Arthur, 1976; Ellertsen et al., 1977; Hunter and Kimbrell, 1980).

Concentrations of microplankton at 100-200 particles l^{-1} were measured on several hauls for the combined size groups of 102-128um and 128-161um (see Fig. 7); while these are relatively rich concentrations compared with previously reported values, they must be considered as underestimates based on the integration of concentrations within the 5m or 10m sampling interval used in this study (see Fig. 7). Incidentally, sampling the same microplankton by conventional oblique net hauls to 60m depth would rarely have revealed concentrations exceeding about 25% of the maxima observed from LHPR sampling (see Fig. 7). Theilacker (1981) reported relatively good survival of morphometrically similar larvae of jack mackerel (*Truchurus symmetricus*) at prey concentrations of 1000 particles l^{-1} but did not determine the level below this at which development was impaired; in the light of the expected and reported critical densities of larval food concentration of about 500 particles l^{-1} for a range of species (see Laurence, 1974), the estimates of 100-200 particles l^{-1} in the present study possibly reflect concentrations in the sea which would be sufficient for survival of mackerel larvae.

The results of this study, therefore, provide general evidence for a functional association between layers of mackerel larvae and microplankton; by implication, these findings give support to the concept of control of larval survival through food availability. One consequence of the suggested importance, for larval feeding, of relatively restricted layers of abundant microplankton is that, to measure food availability, some estimate is required of the occurrence, extent and permanence of such layers; at the same time it is necessary to sample over a wide geographical area to obtain an overall estimate of conditions which are representative for the whole spawning population. In practical terms these opposing scales of sampling present considerable logistic problems.

The occurrence of layers of suitable microplankton may be investigated by sampling at individual stations using systems such as the LHPR, as in these studies, by pumped sampling methods (e.g. Ellertsen et al., 1977) or by some equivalent means of depth-stratified sampling; whichever system is used it is essential to sample for larvae and food particles concurrently, since a relatively small horizontal separation between the larvae and a concentration of microplankton represents an effective barrier, within the limited capability for horizontal movement possessed by the larvae. Fine scale sampling of this kind, at individual stations throughout the spawning area would entail the collection of an excessive number of samples. A more effective strategy is to use high-speed depth-profiling samplers such as the UOR or Batfish (for example, see Herman et al., 1981) to identify areas of potentially favourable conditions for larval survival, using as an index chlorophyll-a concentration or some form of particle count, and to restrict the fine-scale plankton sampling to these areas. An additional advantage of high-speed continuous plankton sampling is that the integration of sampling, reduces both the bias, which results from treating a single station as representative of a wider area, and the variance arising from the patchy distribution of plankton; thus, for example, quantitative surveys of fish eggs, and hence estimation of spawning stock size, can be carried out at high speed, involving the collection of a relatively small amount of material which can give a better estimate of population abundance than by more conventional methods (Anon, 1982).

ACKNOWLEDGEMENTS

The authors would like to acknowledge the opportunity offered by the Fisheries Laboratory, Lowestoft (Ministry of Agriculture Fisheries and Food) and the Marine Laboratory, Aberdeen (Department of Agriculture and Fisheries for Scotland) to participate in their research cruises. Additional acknowledgements are due to Dr. K.R. Clarke for statistical treatment of the data and to Dr. J. Aiken, Mr A.W. John and Mr R.K. Pipe for collaboration in various aspects of the programme.

This work forms part of the programme of the Institute for Marine Environmental Research, a component body of the Natural Environment Research Council, and is supported, in part, by the Ministry of Agriculture, Fisheries and Food.

REFERENCES

Aiken, J. 1981a. A chlorophyll sensor for automatic, remote, operation in the marine environment. Mar.Ecol.Prog.Ser. 4:235.

____________. 1981b. The Undulating Oceanographic Recorder Mark 2. J.Plankton Res. 3(4):551.

Anon. 1982. Report of the working group on larval fish ecology, Lowestoft, England, 3-6 July 1981. Cons.int.Explor.Mer. L3 (Mimeo).

Arthur, D.K. 1976. Food and feeding of larvae of three fishes occurring in the California current, Sardinops sagax, Engraulis mordax, and Trachurus symmetricus. Fish.Bull.U.S. 74(3):517.

____________. 1977. Distribution, size and abundance of microcopepods in the California current system and their possible influence on survival of marine teleost larvae. Fish.Bull.U.S. 75(3):601.

Beers, J.R. and G.L. Stewart. 1969. Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Mar.Biol. 4:182.

Coombs, S.H., R.K. Pipe and C.E. Mitchell. 1981a. The vertical distribution of eggs and larvae of blue whiting (Micromesistius poutassou) and mackerel (Scomber scombrus) in the eastern North Atlantic and North Sea. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:188.

Coombs, S.H., J. Aiken and S.J. Lockwood. 1981b. A survey of mackerel spawning and environmental conditions in the Celtic Sea in May 1981. Cons.int.Explor.Mer. H32 (Mimeo).

Dickson, R.R., P.A. Garbutt and V.N. Pillai. 1980. Satellite evidence of enhanced upwelling along the European continental slope. J.Phys.Oceanog. 10(5):813.

Edinburgh, Oceanographic Laboratory. 1973. Continuous Plankton Records: a plankton atlas of the North Atlantic and the North Sea. Bull.Mar.Ecol. 7.

Ellertsen, B., E. Moksness, P. Solemdal, T. Strømme, S. Tilseth, T. Westgård and V. Øiestad. 1977. Vertical distribution and feeding of cod larvae in relation to occurrence and size of prey organisms. Cons.int.Explor.Mer. L33 (Mimeo).

Field, J.G., K.R. Clarke and R.M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Mar.Ecol.Prog.Ser. 8:37.

Garrod, D.J. and J.M. Colebrook. 1978. Biological effects of variability in the North Atlantic Ocean. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 173:128.

Grave, H. 1978. Feeding of mackerel larvae and early juveniles in the central North Sea. Cons.int.Explor.Mer. H14 (Mimeo).

Gulland, J.A. 1965. The stability of fish stocks. J.du Cons. 37(3):199.

Herman, A.W., D.D. Sameoto and A.R. Longhurst. 1981. Vertical and horizontal distribution patterns of copepods near the shelf break south of Nova Scotia. Can.J.Fish.Aquat.Sci. 38:1065.

Holligan, P.M. and D.A. Harbour. 1977. The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. J.Mar.Biol.Ass.U.K. 57:1075.

Houde, E.D. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull.Mar.Sci. 28(3):395.

Hunter, J.R. and C.A. Kimbrell. 1980. Early life history of Pacific mackerel, Scomber japonicus. Fish Bull.U.S. 78(1):89.

Kendall, M.G. 1955. "Rank correlation methods". Griffin, London.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish Bull.U.S. 73(3):453.

Last, J.M. 1980. The food of twenty species of fish larvae in the west-central North Sea. Tech.Rep.Fish.Lab., Lowestoft. No. 60.

Laurence G.C. 1974. Growth and survival of haddock (Melanogrammus aegelfinus) larvae in relation to planktonic prey concentration. J.Fish.Res.Bd.Canada. 31:1415.

____________. 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, Pseudopleuronectes americanus, larvae during the period from hatching to metamorphosis. Fish Bull.U.S. 75(3):529.

Lockwood, S.J., I.G. Baxter, J.C. Gueguen, G. Joakimsson, R. Grainger, A. Eltink and S.H. Coombs. 1981. The western mackerel spawning stock estimate for 1980. Cons.int.Explor.Mer. H13 (Mimeo).

Longhurst, A.R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res. 23:729.

Longhurst, A.R. and R. Williams. 1976. Improved filtration systems for multiple-serial plankton samplers and their deployment. Deep-Sea Res. 23:1067.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. pp.3-19. In The Early Life History of Fish (J.H.S. Blaxter, ed.) Springer-Verlag, Berlin.

Nellen, Von. W. and G. Hempel. 1970. Beobachtungen am Ichthyoneuston der Nordsee. Ber.Dt.wiss. Kommn.Meeresforsch. 21:311.

O'Connell. C.P. and L.P. Raymond. 1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (Engraulis mordax Girard) in the laboratory. J.Exp.Mar.Biol.Ecol. 5:187.

Owen, R.W. 1981. Microscale plankton patchiness in the larval anchovy environment. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:364.

Pingree, R.D. and G.T. Mardell. 1981. Slope turbulence, internal waves and phytoplankton growth at the Celtic Sea shelf-break. Phil.Trans.R.Soc.Lond.A. 302:663.

Southward, A.J. and B.McK. Bary. 1980. Observations on the vertical distribution of eggs and larvae of mackerel and other teleosts in the Celtic Sea and on the sampling performances of different nets in relation to stock evaluation. J.Mar.Biol.Ass.U.K. 60:295.

Steele, J.A. (ed.). 1978. Spatial Pattern in Plankton Communities. Plenum Press. New York.

Theilacker, G.H. 1981. Effect of feeding history and egg size on the morphology of jack mackerel. Trachurus symmetricus, larvae, Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:432.

Werner, R.G. and J.H.S. Blaxter. 1980. Growth and survival of larval herring (Clupea harengus) in relation to prey density. Can.J.Fish.Aquat.Sci. 37:1063.

Williams, R., N.R. Collins, and D.V.P. Conway (in press). The double LHPR system - a high speed micro - and macro-plankton sampler. Deep-Sea Res.

FLUCTUACIONES DE POBLACIONES DE AVES GUANERAS EN EL LITORAL PERUANO, 1960-1981

Por

Humberto Tovar

Instituto del Mar del Perū (IMARPE)
Apartado 22
Callao
Perū

Summary

The fluctuations of guano bird populations and proportional compositions of guanay, boobies and pelicans are analysed for the years 1960 to 1981. These fluctuations are related with climatic phenomena, El Niño and the amount of anchoveta captured as causes of reduced food available to the birds and the rates of mortality of adults and chicks.

INTRODUCCION

En el Perú la evaluación de poblaciones de aves guaneras de las tres especies más importantes: guanay (*Phalacrocorax bougainvillii*), piquero (*Sula variegata*) y alcatraz (*Pelecanus thagus*), se viene efectuando mediante el método del censo gráfico, cuyos resultados fueron dados a conocer por Jordán (1963), Jordán y Fuentes (1964 y 1966), Fuentes (1969) y Tovar (1978) con datos analizados hasta el ciclo reproductivo 1973/74.

Los censos gráficos de las aves guaneras tienen la finalidad de determinar la magnitud poblacional de cada ciclo reproductivo y conocer sus fluctuaciones, las que están relacionadas con los cambios ecológicos, tal como el Fenómeno "El Niño", que se presenta en el litoral peruano más o menos en forma cíclica y que actúan como un factor limitante natural de la población aviar. En los últimos años el desarrollo acelerado de la pesquería de la anchoveta se ha convertido en otro factor limitante extranatural. Estos dos factores limitantes han ocasionado el descenso de la población de aves guaneras a niveles muy bajos, de los que hasta la fecha no puede recuperarse, permaneciendo relativamente estacionaria.

En el presente trabajo se hace referencia a los análisis realizados anteriormente para los ciclos reproductivos 1960/61 a 1973/74 y se analizan los datos correspondientes a los ciclos reproductivos de 1974/75 a 1980/81.

MATERIAL Y METODOS

El material considerado para la evaluación poblacional de aves guaneras en el período 1974-1981 estuvo constituido por 14 censos gráficos, con dos censos para cada ciclo reproductivo y los censos se llevaron a cabo en las siguientes fechas:

Ciclo reproductivo 1974/75:	20 noviembre 1974 y 15 febrero 1975
Ciclo reproductivo 1975/76:	20 noviembre 1975 y 10 marzo 1976
Ciclo reproductivo 1976/77:	10 diciembre 1976 y 20 febrero 1977
Ciclo reproductivo 1977/78:	10 diciembre 1977 y 10 marzo 1978
Ciclo reproductivo 1978/79:	20 noviembre 1978 y 20 febrero 1979
Ciclo reproductivo 1979/80:	10 diciembre 1979 y 10 marzo 1980
Ciclo reproductivo 1980/81:	10 diciembre 1980 y 10 marzo 1981

El citado material se obtuvo gracias a la cooperación de Pesca Perú, Subdivisión Fertilizantes, quien tiene a su cargo la administración de Islas y puntas guaneras del litoral peruano (Fig. 1).

Se siguió el método descrito por Jordán (1963) que se puede resumir como sigue: en la fecha y hora señalada para el censo, se grafican los contornos de las colonias de aves en cada isla y punta guanera en los croquis respectivos, indicando para cada especie la zona ocupada por aves en proceso reproductivo y en reposo; la información incluye además apreciaciones numéricas de las aves localizadas en barrancos y pequeños islotes fuera del croquis; luego empleando un planímetro se efectúa una lectura de cada una de las colonias graficadas, dichas lecturas se convierten a metros cuadrados multiplicando por el coeficiente pre-determinado para cada isla y punta; una vez obtenida el área, el cálculo del número de aves y la interpretación se efectúa a base de una escala de densidades promedio para cada especie. El cómputo final en cada lugar se efectuó considerando por separado adultos y polluelos, aves en reproducción y aves en reposo; los individuos apreciados en barrancos e islotes son agregados en cada caso.

El empleo del mismo método permite efectuar comparaciones de las poblaciones a través de los años y analizar las fluctuaciones de las mismas.

Con el fin de obtener resultados más confiables sobre poblaciones de aves guaneras en cada ciclo reproductivo, se efectuaron dos censos gráficos, uno al inicio y otro al finalizar la fase reproductiva para así tener una idea más concreta de la población aviar.

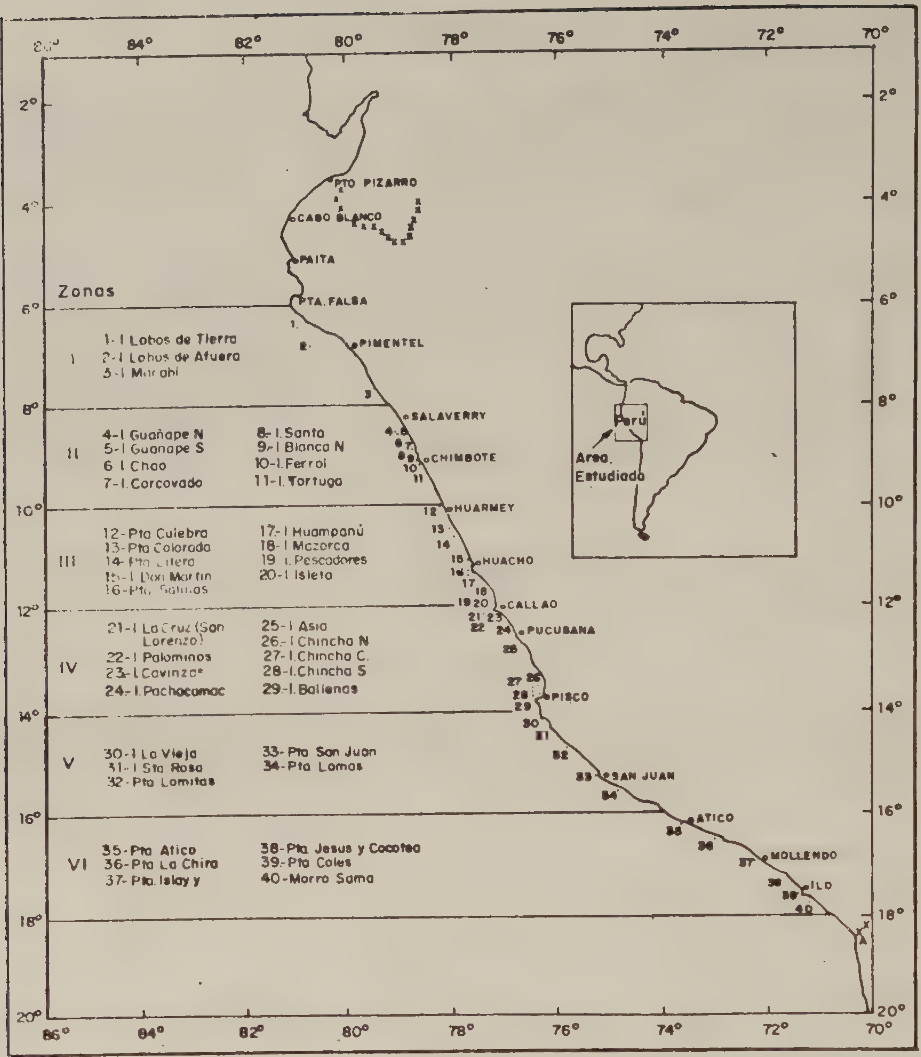

86°
84°
82°
80°
78°
76°
74°
72°
70°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°
PTO PIZARRO
CABO BLANCO
PAITA
PTA. FALSA
PIMENTEL
SALAVERRY
CHIMBOTE
HUARMEY
HUACHO
CALLAO
PUCUSANA
PISCO
SAN JUAN
ATICO
MOLLENDO
ILO
Zonas
I
1- I Lobos de Tierra
2- I Lobos de Afuera
3- I Macabi
II
4- I Guañape N
5- I Guanape S
6 I Chao
7- I. Corcovado
8- I. Santa
9- I Blanca N
10- I. Ferrol
11- I. Tortuga
III
12- Pta Culebra
13- Pta Colorada
14- Pta Litera
15- I Don Martin
16- Pta. Salinas
17- I Huampanú
18- I Mazorca
19 I. Pescadores
20- I Isleta
IV
21- I La Cruz (San Lorenzo)
22- I Palominos
23- I. Cavinzas
24- I. Pachacamac
25- I Asia
26- I Chincha N
27- I. Chincha C.
28- I. Chincha S
29- I. Ballenas
V
30- I La Vieja
31- I Sta Rosa
32- Pta Lomitas
33- Pta San Juan
34- Pta Lomas
VI
35- Pta Atico
36- Pta La Chira
37- Pta. Islay y
38- Pta. Jesus y Cocotea
39- Pta Coles
40- Morro Sama
Perú
Area Estudiada

Fig. 1.-Ubicacion de Islas y Puntas Guaneras del litoral peruano con división en zonas de 2° Lat. Sur.

Tabla 1. Aves guaneras adultas en cada ciclo reproductivo, a base de censos gráficos (en millones).

CICLO REPRODUCTIVO	GUANAY		PIQUERO		ALCATRAZ		TOTAL (millones)
	Cantidad	%	Cantidad	%	Cantidad	%	
1960/61	9.44	75	2.85	23	0.27	2	12.56
1961/62	13.70	80	2.99	18	0.32	2	17.01
1962/63	14.89	82	2.76	15	0.42	2	18.07
1963/64	12.46	85	2.13	14	0.12	1	14.72
1964/65	13.46	82	2.82	17	0.23	1	16.51
1965/66	3.12	71	1.02	23	0.24	6	4.38
1966/67	2.92	63	1.33	28	0.42	9	4.44
1967/68	2.86	66	1.19	28	0.26	6	4.31
1968/69	3.21	61	1.76	34	0.26	5	5.24
1969/70	3.07	65	1.43	30	0.24	5	4.74
1970/71	2.69	59	1.54	34	0.30	7	4.52
1971/72	4.24	66	1.77	27	0.46	7	6.47
1972/73	0.84	46	0.80	44	0.17	9	1.81
1973/74	1.02	41	1.14	45	0.35	14	2.52
1974/75	1.03	42	1.06	43	0.37	15	2.46
1975/76	1.29	37	1.79	51	0.43	12	3.51
1976/77	1.14	38	1.62	53	0.28	9	3.04
1977/78	1.68	38	2.20	49	0.58	13	4.46
1978/79	2.06	36	3.03	53	0.63	11	5.72
1979/80	2.10	40	2.45	47	0.69	13	5.24
1980/81	2.29	44	2.34	45	0.58	11	5.21

RESULTADOS

Estimados de las Poblaciones (Tabla 1, Fig. 2)

Los resultados de las evaluaciones de las aves guaneras hasta el ciclo reproductivo 1973/74 fueron dadas a conocer por Tovar (1978) citando como nivel poblacional para el referido ciclo reproductivo 2.52 millones de aves cuya composición por especies fue 45, 41 y 14% de piquero, guanay y alcatraz, respectivamente. Durante el ciclo 1974/75, la población se mantuvo relativamente en el mismo nivel. En cambio, durante el ciclo reproductivo 1975/76, la magnitud poblacional fue de 3.51 millones que representan un incremento del 43%; durante el ciclo 1976/77, como consecuencia de anomalías térmicas en la superficie del mar, hubo una disminución de medio millón de aves, llegando a 3.04 millones de aves compuesto por 53, 38 y 9% de piquero, guanay y alcatraz, respectivamente. Como consecuencia del notable afloramiento en la costa peruana, principalmente al sur de 14°S en 1978, las aves guaneras aumentaron su nivel poblacional hasta 4.46 millones en el ciclo reproductivo 1977/78, el ascenso poblacional continuó en el ciclo reproductivo 1978/79, llegando al nivel de 5.72 millones, constituido por 53, 36 y 11% de piquero, guanay y alcatraz o pelícano, respectivamente. La población durante el ciclo reproductivo 1979/80 fue de 5.04 millones, el doble que en 1973/74, manteniéndose la composición por especies en los mismos niveles.

Durante el ciclo reproductivo 1980/81, el nivel poblacional llegó a 5.21 millones, constituido por 45, 55 y 11% de piquero, guanay y alcatraz, respectivamente.

Para una mejor comprensión de la situación poblacional de las aves, se analizan en forma independiente cada una de las especies de aves guaneras.

La población de guanay:

Para analizar la fluctuación poblacional de guanay se consideró como punto de referencia el ciclo reproductivo 1960/61 con 9.44 millones de aves adultas, en 1961/62 la población fue estimada en 13.70 millones y en 1962/63 continuó el ascenso de la población de guanay llegando al nivel de 4.89 millones; pero en el ciclo reproductivo 1963/64 se produce una considerable mortandad de aves a consecuencia de alteraciones en las condiciones oceanográficas que según Jordán y Fuentes (1966) determinaron cambios en la distribución vertical de la anchoveta haciéndola inaccesible a las aves. En este ciclo reproductivo el nivel poblacional de guanay se estimó en 3.12 millones, permaneciendo estacionario en cerca de 3 millones hasta el ciclo reproductivo 1970/71, con un ascenso hasta 4.24 millones en 1971/72. A consecuencia del Fenómeno "El Niño" de 1972, esta población descendió a 0.84 millones en el ciclo 1972/73, ascendiendo a 1.02 millones en 1973/74, donde permaneció estacionaria con ligeras variaciones hasta 1976/77. A partir de 1977/78 comenzó el ascenso llegando a 2.29 millones en 1980/81.

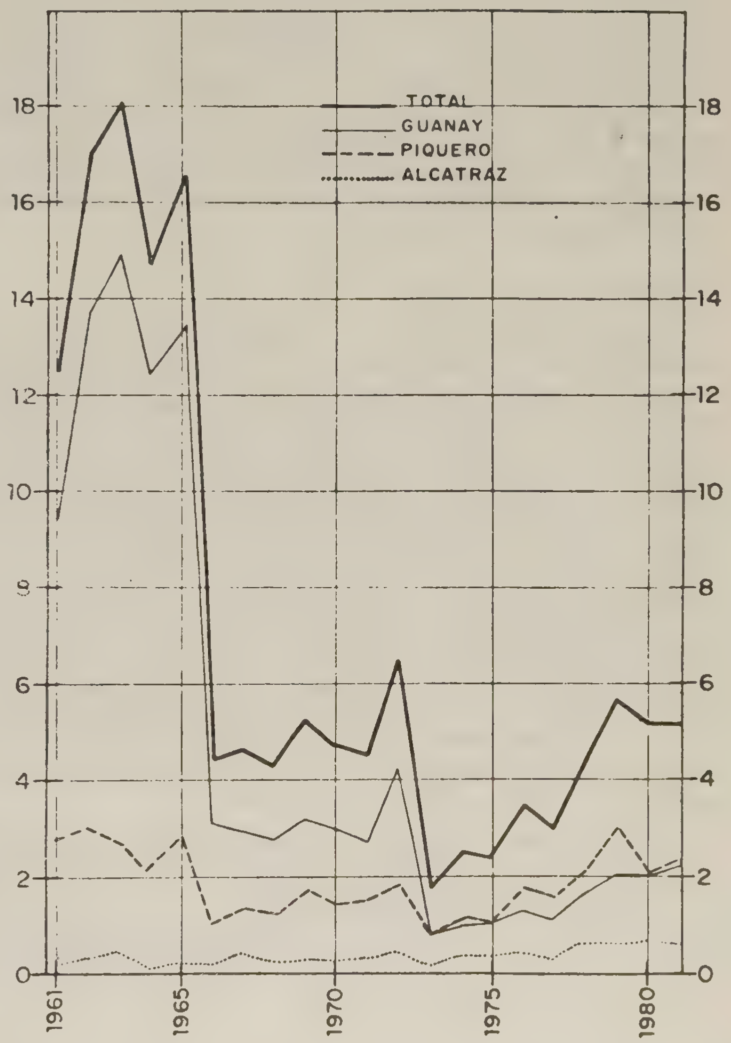


Fig. 2.- Aves guaneras adultas en cada ciclo reproductivo.

Población de piquero:

El piquero es otra de las especies productoras del fertilizante orgánico conocido como "guano de islas".

De la misma forma que para la especie anterior, para el piquero se parte del nivel poblacional del ciclo reproductivo 1060/61 con 2.85 millones, notando un ligero aumento de 0.14 millones en 1961/62; en los siguientes años se nota un descenso poblacional llegando a su nivel más crítico en 1972/73 con 0.80 millones que representa sólo el 28% de la población inicial. La población llegó a este nivel crítico a consecuencia del Fenómeno "El Niño" en 1972, que produjo una depresión ecológica en el mar peruano. Una ves normalizadas las condiciones ambientales marinas, el nivel poblacional comenzó a recuperarse; inclusive en 1978/79 llegó a superar el nivel inicial en 5%, descendiendo nuevamente en los siguientes ciclos reproductivos, llegando a 1980/81 con 2.34 millones.

Población de alcatraz o pelícano:

Cuantitativamente el alcatraz es la especie de menor importancia por su reducido nivel poblacional ocupando normalmente el tercer lugar después del guanay y piquero; además produce un fertilizante de baja calidad.

Durante el ciclo reproductivo 1960/61, el nivel poblacional de alcatraz llegó a 0.27 millones de aves. En los ciclos reproductivos 1963/64 y 1972/73 la población bajó hasta 0.12 y 0.17 millones de aves respectivamente; aparentemente las alteraciones del medio ambiente marino no ocasionaron fluctuaciones de tanta consideración como ocurrió principalmente en guanay. Por el contrario, en los últimos años de la década del 70 se nota un aumento considerable de la población llegando a 1980/81 con 0.58 millones, que representa un aumento del nivel poblacional en más del 100% con respecto a 1960/61, sugiriendo que el alcatraz es la única especie que no fue afectada por los altos volúmenes de captura de anchoveta para la industria y las alteraciones del medio ambiente marino ocurridos en los últimos años.

Composición por Especies (Tabla 1, Fig. 3)

Hay evidencias que desde tiempos remotos, el guanay siempre predominó entre las especies de aves productoras de guano de islas. Vogt (1942) cita en orden de importancia primero al guanay seguido de piquero y alcatraz; la Compañía Administradora de Guano (1954) refiere que el guanay produce el 85% del fertilizante; Gamarra (1955) al analizar datos de 1946, obtiene como resultado los porcentajes de 81, 17 y 2% correspondientes al guanay, piquero y alcatraz, respectivamente; Jordán (1963) para el ciclo reproductivo 1961/62 obtiene los siguientes porcentajes: guanay 80%, piquero 18% y alcatraz 2%; Jordán y Fuentes (1965) también refieren que la composición por especies fue de 82, 15 y 2% de guanay, piquero y alcatraz, respectivamente; Fuentes (1969) al analizar datos del ciclo reproductivo 1968/69, determina que la población de aves guaneras estuvo compuesta por 58, 37 y 5% de guanay, piquero y alcatraz, indicando que la composición por especies de la población de aves guaneras estaba cambiando; Tovar (1978) al analizar datos del ciclo reproductivo 1973/74, determinó que el piquero llegó al primer lugar con 45%, guanay con 41% y alcatraz con 14%. Las últimas evaluaciones de poblaciones indican que el guanay continuó descendiendo, llegando a 1978/79 con 53, 36 y 11% de piquero, guanay y alcatraz, respectivamene; durante 1980/81 los niveles porcentuales fueron de 45, 44 y 11% de piquero, guanay y alcatraz, respectivamente.

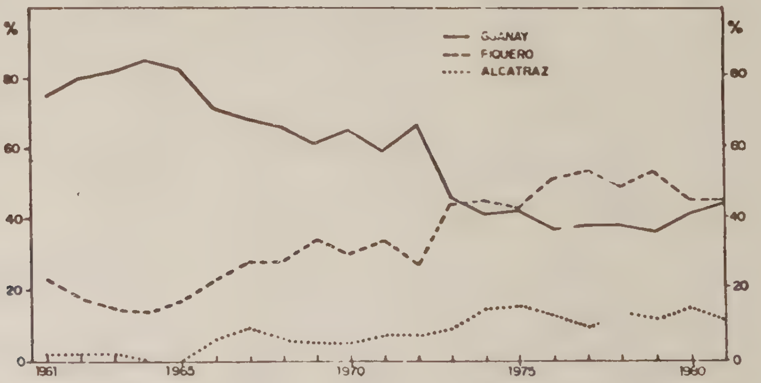


Fig. 3.- Composición por especies de la población de aves guaneras en cada ciclo reproductivo de 1960/61 a 1980/81.

Estos significativos cambios en la composición por especies se hallan íntimamente relacionados a la escasa disponibilidad de recurso anchoveta que a su vez está relacionado con las alteraciones de las condiciones ambientales marinas, más conocidas como Fenómeno "El Niño" y el desarrollo acelerado de la pesquería de anchoveta. La anchoveta es el alimento principal del guanay, mientras que las otras dos especies de aves guaneras pueden cambiar o reemplazar la anchoveta por otros peces y lógicamente por esta razón, el guanay fue la especie más afectada por la reducción de la población de anchoveta.

Alimentación

El alimento, como en cualquier comunidad zoológica, es fundamental; y en el caso específico de las aves guaneras, desempeñó un rol muy importante en el normal desarrollo poblacional y composición específica.

Según Vogt (1942), la presencia de grandes bandadas de aves obedecen a la presencia de grandes cardúmenes de anchoveta, Avila (1954) y Jordán (1959) refieren que el guanay se alimenta principalmente de anchoveta. Sin embargo, es necesario tener presente que las referidas investigaciones fueron realizadas cuando el recurso anchoveta se hallaba en su fase inicial de explotación; es decir, que la anchoveta era abundante y se encontraba disponible para las aves. Pero el desarrollo acelerado de la industria de la harina de anchoveta obligó a capturar cada año mayores volúmenes de anchoveta, convirtiendo al hombre en un desleal competidor de las aves, ahondando más el problema. Los cambios temporales y cíclicos de las condiciones ambientales marinas a causa del fenómeno conocido como "El Niño", influyeron también poderosamente en las fluctuaciones de poblaciones de aves.

Tovar (en prensa) determinó que en septiembre y octubre de 1977, durante la escasez de anchoveta, las aves estuvieron alimentándose de otras especies ícticas como: lorna (*Sciaena deliciosa*), anchoveta blanca (*Anchoa* sp.), coco (*Paralonchurus peruanus*), cabinza (*Isacia conceptionist*), (*Bagre* sp.), anchoveta (*Engraulis ringens*), ayanque o cachema (*Cynoscion analis*), corvinilla (*Sciaena gilberti*) y otras seis especies más; mientras que a partir de noviembre de 1977 a marzo de 1978, nuevamente el guanay estuvo alimentándose de anchoveta.

Estas faltas de disponibilidad del recurso anchoveta para la alimentación de las aves guaneras originaron fluctuaciones y cambios en la composición por especies, porque cada una de las tres especies tienen diferentes modalidades para obtener su alimento: a) el guanay busca su alimento en grandes bandadas y precisa de cardúmenes grandes de anchoveta, la captura la efectúan mediante buceos y son más dependientes del recurso anchoveta, razón por la cual la población de guanay bajó considerablemente por la escasez de anchoveta y de la cual hasta ahora no puede recuperarse; b) el piquero busca su alimento en pequeñas bandadas y lógicamente necesita de pequeños cardúmenes, dependiendo en menor grado de la disponibilidad de anchoveta; la captura la realizan mediante descensos rápidos y en picada desde aproximadamente 40 metros de altura ; y c) el alcatraz o pelícano, a semejanza del piquero, no depende de grandes cardúmenes y pesca en forma solitaria. Además está incapacitado para bucear por tener sacos aéreos en el pectoral y cuello, razón por la cual esta especie se alimenta de peces que se hallan en la superficie, además están capacitados para alimentarse de peces más grandes; es posible que ésto motivó que la población de esta especie no fuera afectada, por el contrario la poblacional ha aumentado.

Exito reproductivo (Tabla 2, Fig. 4)

El ciclo reproductivo de las aves guaneras se halla íntimamente relacionado a la época de mayor y mejor disponibilidad de los recursos ícticos, principalmente de la anchoveta; por esta razón, el ciclo reproductivo de las aves comienza generalmente en noviembre de cada año y concluye en febrero-marzo del siguiente año, teniendo en cuenta que el guanay necesita de cuatro meses para cumplir su ciclo reproductivo, un mes de celo, un mes de incubación, incluido la postura, y dos meses de cuidado de los pichones.

Tabla 2a, Porcentaje de reproducción de aves guaneras a base de censos gráficos.

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE REPRODUCCION
	ADULTOS	POLLUELOS	
1960/61	12.56	4.91	39
1961/62	17.01	11.76	69
1962/63	18.07	12.84	71
1963/64	14.72	6.01	41
1964/65	16.51	8.60	52
1965/66	4.38	0.04	1
1966/67	4.64	2.09	47
1967/68	4.31	1.58	37
1968/69	5.24	2.00	35
1969/70	4.74	2.10	44
1970/71	4.52	1.85	41
1971/72	6.47	2.80	43
1972/73	1.81	0	0
1973/74	2.52	0.70	28
1974/75	2.46	0.64	26
1975/76	3.51	0.90	26
1976/77	3.04	0.58	25
1977/78	4.46	0.96	22
1978/79	5.72	1.31	23
1979/80	5.24	1.79	35
1980/81	5.21	1.90	36

Tabla 2b Cantidad de polluelos en cada ciclo reproductivo a base de censos gráficos (en millones).

CICLO	GUANAY		PIQUERO		ALCATRAZ		TOTAL
REPRODUCTIVO	Cantidad	%	Cantidad	%	Cantidad	%	
1960/61	3.76	76	1.06	22	0.09	2	4.91
1961/62	9.08	78	2.30	19	0.38	3	11.76
1962/63	10.53	82	1.93	15	0.38	3	12.84
1963/64	5.75	96	0.22	3	0.04	1	6.01
1964/65	6.47	75	2.00	23	0.13	2	8.60
1965/66	0.004	9	0.03	68	0.01	23	0.04
1966/67	1.27	61	0.51	24	0.31	15	2.09
1967/68	0.92	58	0.51	32	0.15	10	1.58
1968/69	0.99	49	0.92	46	0.09	5	2.00
1969/70	1.57	75	0.37	17	0.16	8	2.10
1970/71	1.15	62	0.58	31	0.12	7	1.85
1971/72	1.78	64	0.61	22	0.41	15	2.80
1972/73	0	0	0	0	0	0	0
1973/74	0.12	17	0.54	77	0.04	6	0.70
1974/75	0.17	27	0.32	50	0.15	23	0.64
1975/76	0.61	68	0.27	30	0.02	2	0.90
1976/77	0.14	24	0.33	57	0.11	19	0.58
1977/78	0.40	42	0.26	27	0.30	31	0.96
1978/79	0.55	42	0.57	43	0.19	15	1.31
1979/80	0.65	21	1.09	78	0.05	2	1.79
1980/81	1.03	54	0.74	39	0.13	7	1.90

El éxito reproductivo se determinó a base de la información sobre estado reproductivo que incluyen en los censos mediante gráficos de áreas ocupadas por aves con pichones y huevos; pero el éxito reproductivo depende de magnitud y disponibilidad de las fuentes de alimentación.

La tasa de reproducción fue calculado a base de la proporción de polluelos con respecto al total de adultos en cada ciclo reproductivo.

La tasa de reproducción en 1960/61 fue de 39%, llegando a 1962/63 con 71% que representa la tasa más alta porque en los siguientes años fue descendiendo. Inclusive durante 1965 y 1972, a causa de anomalías oceanográficas en el mar peruano, las tasas de reproducción fueron bajísimas. Después de 1972 las tasas de reproducción no llegaron al 30% a excepción de 1979/80 y en 1980/81 que fue de 35% y 36% como se verá más adelante, muchas veces estas tasas de reproducción no se concretan en un incremento.

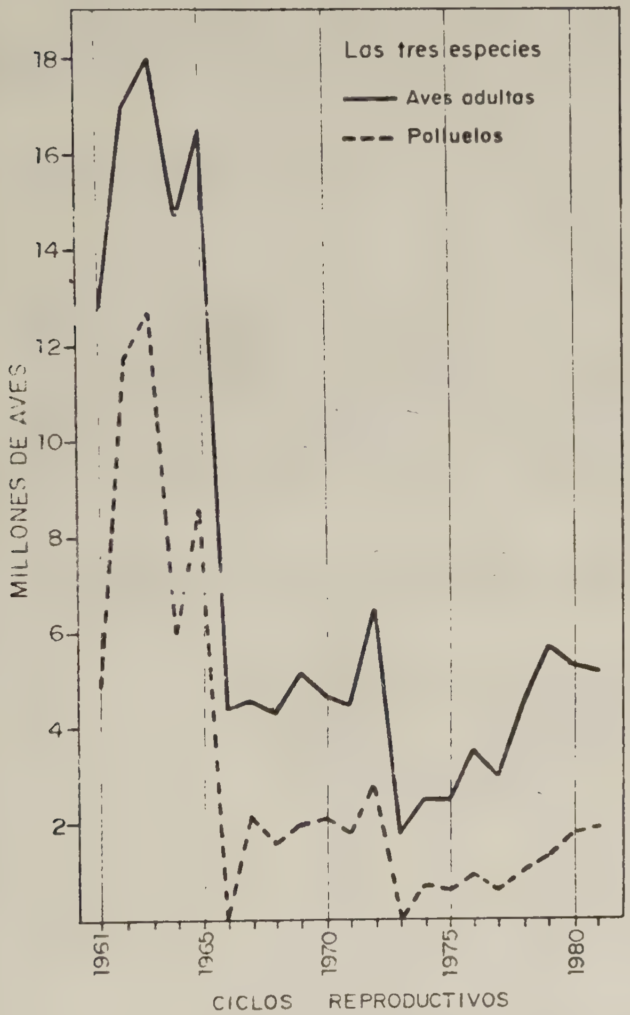


Fig. 4a.- Aves adultas y polluelos en cada ciclo reproductivo, a base de censos gráficos.

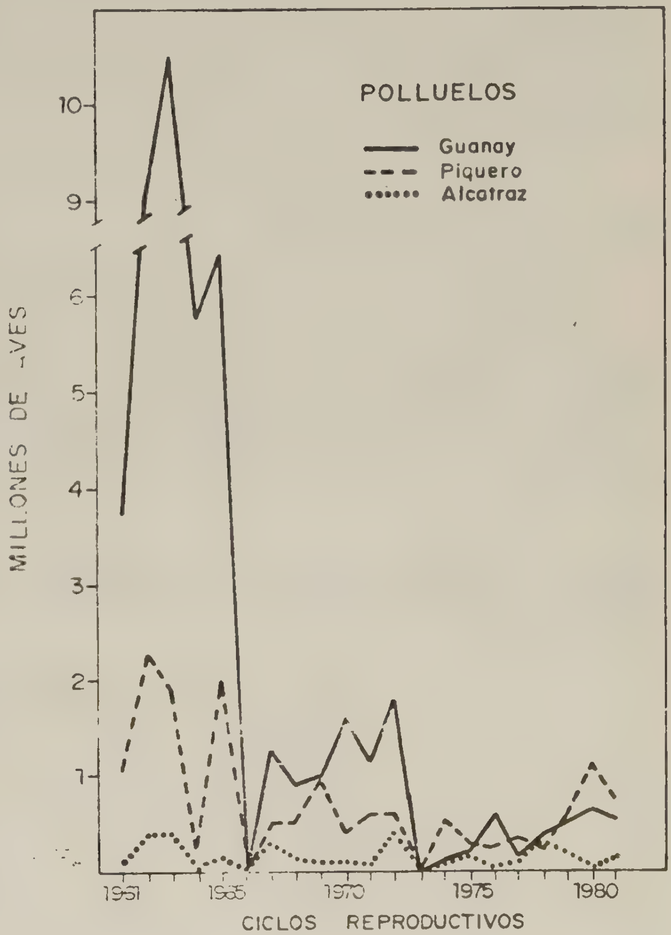


Fig. 4b.- Cantidad de polluelos en cada ciclo reproductivo.

Reproducción de guanay (Tabla 3, Fig. 5) :

Debido a la mortalidad de aves ocurrida en 1957/58 a causa del fenómeno oceanográfico conocido como "El Niño", la población quedó reducida estimándose en 1960/61 en 9.44 millones. En este ciclo el porcentaje de reproducción fue del 40%; en los siguientes dos años aumentó a 70% en 1962/63 luego disminuyó en los siguientes años, e inclusive durante 1965 y 1972, a causa de anomalías oceanográficas, el porcentaje de reproducción fue cero; a partir de 1972/73 se acentuó más el descenso del porcentaje de reproducción de guanay con 31% en 1979/80, para nuevamente ascender a 45% en 1980/81.

Reproducción de piquero (Tabla 4, Fig. 6) :

Efectuando el análisis de la misma forma que para la especie anterior, la población de piqueros tuvo porcentajes de reproducción con 77 y 70% en los años 1961/62 y 1962/63, respectivamente; en los siguientes años los porcentajes fueron descendiendo, llegando a niveles más críticos, de 3% en 1965/66 y cero en 1972/73, a causa de la presencia de anomalías oceanográficas. El porcentaje promedio para 1966/67 y 1971/72 fue de 38%, en los siguientes años, de 1973/74 a 1979/80,que tuvieror como porcentaje de reproducción 19% a excepción de los años 1973/74 y 1979/80 que tuvieron como tasa 47 y 44%, respectivamente. Finalmente, para 1980/81, al porcentaje de reproducción fue de 32%.

Estos datos indican que en los últimos años las tasas anuales de reproducción fueron muy bajas para el piquero.

Reproducción de alcatraz o pelícano (Tabla 5, Fig. 6):

A diferencia de las dos especies anteriores, el alcatraz, estuvo sometida a fluctuaciones muy irregulares, sin embargo es la única especie que tuvo los porcentajes más altos de reproducción, a excepción de 1, 4, 0, 5 y 7% para los años 1961/62, 1965/66, 1972/73, 1975/76 y 1979/80, respectivamente. En los años restantes tuvo una reproducción promedio de 57%, con los procentajes más altos de 90, 89 y 107%,respectivamente, para los años 1962/63, 1971/72 y 1976/77. El nivel poblacional de esta especie fue de 0.42 millones en 1962/63, y en 1980/81 fue de 0.58 millones, con un incremento de 38% en dicho período.

Es necesario aclarar que esta especie puede alimentarse de anchoveta y además de otros peces, incluyendo peces más grandes, por lo cual soporta mejor la ausencia o falta de disponibilidad de anchoveta.

Tabla 3. Porcentaje de reproducción de guanay

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE REPRODUCCION
	ADULTOS	POLLUELOS	
1960/61	9.44	3.76	40
1961/62	13.70	9.08	66
1962/63	14.89	10.53	70
1963/64	12.46	5.75	46
1964/65	13.46	6.47	48
1965/66	3.12	0.004	0
1966/67	2.92	1.27	43
1967/68	2.86	0.92	32
1968/69	3.21	0.99	31
1969/70	3.07	1.57	51
1970/71	2.69	1.15	42
1971/72	4.24	1.78	41
1972/73	0.84	0	0
1973/74	1.02	0.12	12
1974/75	1.03	0.17	15
1975/76	1.29	0.61	47
1976/77	1.14	0.14	12
1977/78	1.68	0.40	24
1978/79	2.06	0.55	27
1979/80	2.10	0.65	31
1980/81	2.29	1.03	45

Tabla 4. Porcentaje de reproducción de piquero.

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE REPRODUCCION
	ADULTOS	POLLUELOS	
1960/61	2.85	1.06	37
1961/62	2.99	2.30	77
1962/63	2.76	1.93	70
1963/64	2.13	0.22	10
1964/65	2.82	2.00	53
1965/66	1.02	0.03	3
1966/67	1.33	0.51	46
1967/68	1.19	0.51	43
1968/69	1.76	0.92	42
1969/70	1.43	0.37	26
1970/71	1.54	0.58	38
1971/72	1.77	0.61	34
1972/73	0.80	0	0
1973/74	1.14	0.54	47
1974/75	1.06	0.32	30
1975/76	1.79	0.27	15
1976/77	1.62	0.33	20
1977/78	2.20	0.26	12
1978/79	3.03	0.57	19
1979/80	2.45	1.09	44
1980/81	2.34	0.74	32

Tabla 5. Porcentaje de reproducción de pelícano o alcatraz.

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE REPRODUCCION
	ADULTOS	POLLUELOS	
1960/61	0.27	0.09	33
1961/62	0.32	0.38	118
1962/63	0.42	0.38	90
1963/64	0.12	0.04	33
1964/65	0.23	0.13	56
1965/66	0.24	0.01	4
1966/67	0.42	0.31	74
1967/68	0.26	0.15	58
1968/69	0.26	0.09	35
1969/70	0.24	0.16	67
1970/71	0.30	0.12	40
1971/72	0.46	0.41	89
1972/73	0.17	0	0
1973/74	0.35	0.04	14
1974/75	0.37	0.15	40
1975/76	0.43	0.02	5
1976/77	0.28	0.11	107
1977/78	0.58	0.30	52
1978/79	0.63	0.19	30
1979/80	0.69	0.05	7
1980/81	0.58	0.13	22

Tabla 6. Porcentajes de incremento y mortalidad de aves guaneras a base de censos gráficos.

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE INCREMENTO (%)	PORCENTAJE DE MORTALIDAD	
	ADULTOS	POLLUELOS		ADULTOS	POLLUELOS
1960/61	12.56	4.91	-	-	-
1961/62	17.01	11.76	35	0	9
1962/63	18.07	12.84	6	0	91
1963/64	14.72	6.01	0	18	100
1964/65	16.51	8.10	12	0	70
1965/66	4.38	0.04	0	73	100
1966/67	4.64	2.09	6	0	0
1967/68	4.31	1.58	0	7	100
1968/69	5.24	2.00	22	0	41
1969/70	4.74	2.10	0	10	100
1970/71	4.52	1.85	0	5	100
1971/72	6.47	2.80	43	0	0
1972/73	1.81	0	0	72	100
1973/74	2.52	0.70	39	0	0
1974/75	2.46	0.64	0	2	100
1975/76	3.51	0.90	43	0	0
1976/77	3.04	0.58	0	13	100
1977/78	4.46	0.96	47	0	0
1978/79	5.72	1.31	28	0	0
1979/80	5.24	1.79	0	12	100
1980/81	5.21	1.90	3	0	0

Tabla 7. Porcentaje de incremento y mortalidad de guanay.

CICLO REPRODUCTIVO	CANTIDAD (en millones)		PORCENTAJE DE INCREMENTO (%)	PORCENTAJE DE MORTALIDAD	
	ADULTOS	POLLUELOS		ADULTOS	POLLUELOS
1960/61	9.44	3.76	-	-	-
1961/62	13.70	9.08	45	0	0
1962/63	14.89	10.53	9	0	87
1963/64	12.46	5.75	0	16	100
1964/65	13.46	6.47	8	0	83
1965/66	3.12	0.004	0	77	100
1966/67	2.92	1.27	0	6	0
1967/68	2.86	0.92	0	2	100
1968/69	3.21	0.99	12	0	62
1969/70	3.07	1.57	0	4	100
1970/71	2.69	1.15	0	12	100
1971/72	4.24	1.78	58	0	0
1972/73	0.84	0	0	80	100
1973/74	1.02	0.12	21	0	0
1974/75	1.03	0.17	1	0	92
1975/76	1.29	0.61	25	0	0
1976/77	1.14	0.14	0	12	100
1977/78	1.68	0.40	47	0	0
1978/79	2.06	0.55	23	0	5
1979/80	2.10	0.65	2	0	92
1980/81	2.29	1.03	9	0	71

Tabla 8. Porcentaje de incremento y mortalidad de piquero.

CICLO REPRODUCTIVO	CANTIDAD (en millones) ADULTOS	CANTIDAD (en millones) POLLUELOS	PORCENTAJE DE INCREMENTO (%)	PORCENTAJE DE MORTALIDAD ADULTOS	PORCENTAJE DE MORTALIDAD POLLUELOS
1960/61	2.85	1.06	-	-	-
1961/62	2.99	2.30	5	0	86
1962/63	2.76	1.93	0	8	100
1963/64	2.13	0.22	0	23	100
1964/65	2.82	2.00	32	0	0
1965/66	1.02	0.03	0	64	100
1966/67	1.33	0.51	30	0	0
1967/68	1.19	0.51	0	10	100
1968/69	1.76	0.92	48	0	0
1969/70	1.43	0.37	0	19	100
1970/71	1.54	0.58	8	0	70
1971/72	1.77	0.61	15	0	60
1972/73	0.80	0	0	55	100
1973/74	1.14	0.54	42	0	0
1974/75	1.06	0.32	0	7	100
1975/76	1.79	0.27	69	0	0
1976/77	1.62	0.33	0	9	100
1977/78	2.20	0.26	36	0	0
1978/79	3.03	0.57	38	0	0
1979/80	2.45	1.09	0	19	100
1980/81	2.34	0.74	0	4	100

Tabla 9. Porcentaje de incremento y mortalidad de pelícano o alcatraz.

CICLO REPRODUCTIVO	CANTIDAD (en millones) ADULTOS	CANTIDAD (en millones) POLLUELOS	PORCENTAJE DE INCREMENTO (%)	PORCENTAJE DE MORTALIDAD ADULTOS	PORCENTAJE DE MORTALIDAD POLLUELOS
1960/61	0.27	0.09	-	-	-
1961/62	0.32	0.38	18	0	44
1962/63	0.42	0.38	31	0	74
1963/64	0.12	0.04	0	71	100
1964/65	0.23	0.13	92	0	0
1965/66	0.24	0.01	4	0	92
1966/67	0.42	0.31	75	0	0
1967/68	0.26	0.15	0	38	100
1968/69	0.26	0.09	0	0	100
1969/70	0.24	0.16	0	8	100
1970/71	0.30	0.12	8	0	100
1971/72	0.46	0.41	53	0	0
1972/73	0.17	0	0	63	100
1973/74	0.35	0.04	105	0	0
1974/75	0.37	0.15	6	0	60
1975/76	0.43	0.02	16	0	60
1976/77	0.28	0.11	0	35	100
1977/78	0.58	0.30	107	0	0
1978/79	0.63	0.19	9	0	83
1979/80	0.69	0.05	9	0	68
1980/81	0.58	0.13	0	16	100

Tabla 10. **Poblaciones de aves guaneras y volumen de captura total anual de anchoveta.**

AÑOS	TOTAL AVES (millones)	ANCHOVETA * millones de TMB
1961	12.6	4'579,708
1962	17.0	6'274,624
1963	18.1	6'423,243
1964	14.7	8'863,367
1965	16.5	7'233,479
1966	4.4	8'529,820
1967	4.6	9'824,623
1968	4.3	10'262,661
1969	5.2	8'960,460
1970	4.7	12'276,977
1971	4.5	10'281,784
1972	6.5	4'448,511
1973	1.8	1'512,828
1974	2.5	3'583,449
1975	2.5	3'078,804
1976	3.5	3'863,049
1977	3.0	792,085
1978	4.5	1'187,041
1979	5.7	1'362,760
1980	5.1	565,842
1981	5.2	1'163,000

* **Datos de la Dirección de Estadística y Economía de IMARPE.**

Incremento y Mortalidad (Tabla 6, Fig. 7)

La evaluación de poblaciones de aves guaneras desde hace veinte años, mediante el método del censo gráfico, demuestra que el incremento de la población se halla en relación directa al éxito en cada ciclo reproductivo y la posterior supervivencia de polluelos; por esta razón se considera que el incremento de aves adultas se realiza a base de los polluelos del ciclo reproductivo anterior que sobrevivieron un año. Anteriormente ya se dijo que el éxito reproductivo, y en este caso, la supervivencia de polluelos se halla íntimamente ligado a la disponibilidad de las fuentes de alimentación; cuando estas fuentes de alimentación escasean, ocurren mortandades de adultos y juveniles. A base de estas consideraciones se elaboró la Tabla 6; en ella se puede apreciar que de los 20 años analizados en doce de ellos hubo incremento. Los incrementos mayores, con 4.45, 1.79 y 1.95 millones de aves fueron en los años 1961/62, 1964/65 y 1971/72, respectivamente. En los años restantes, los incrementos fueron de menor consideración. En cambio, durante los otros ocho años no consecutivos hubo mortalidades de adultos y polluelos, siendo los más graves los ocurridos en 1963/64, 1965/66 y 1972/73 con 3.35, 12.13 y 4.66 millones, respectivamente. Estas mortalidades concuerdan con los años en que ocurrieron anomalías oceanográficas en el mar peruano a causa del Fenómeno "El Niño". Con respecto a los polluelos se notó las más altas mortalidades durante los años 1962/63, 1963/64, 1964/65 y 1965/66 con 10.70, 12.84, 4.22 y 8.10 millones respectivamente.

En 1979/80 hubo una mortalidad de 0.65 millones de adultos y 1.31 millones de polluelos.

Incremento y mortalidad de guanay (Tabla 7, Fig. 8):

Los estimados de la población de guanay, evaluada de 1960-1981, permitió conocer mejor que el guanay estuvo sujeto a fluctuaciones de consideración a causa de incremento en unos años y mortalidad en otros.

Los mayores incrementos en la población de guanay se produjeron durante los ciclos reproductivos de 1961/62, 1971/72 y 1977/78 con 45, 58 y 47%, respectivamente, incrementos menores ocurrieron durante los ciclos reproductivos de 1968/69, 1973/74, 1975/76 y 1978/79 con 12, 21, 25 y 26%, respectivamente. Estos incrementos estarían indicando que existe un mecanismo de compensación en la población de guanay, porque estos incrementos se produjeron antes y después de períodos con mortalidades altas.

Estos descensos en los niveles poblacionales debidos a mortalidad ocurrieron principalmente a causas de alteraciones del medio ambiente marino, principalmente en 1965/66 y 1972/73 con mortalidades del 77 y 80% de la población, respectivamente; los períodos donde los porcentajes de mortalidad no fueron tan altos, estuvieron asociados a los altos volúmenes de captura de anchoveta para la industria, que disminuyó considerablemente y en forma gradual la disponibilidad de anchovetas para alimento de guanay, lo cual inclusive no permitió la recuperación del nivel poblacional después de cada mortalidad.

La población de guanay en 1980/81 representó sólo el 16% de la que existió en 1962/63. La reproducción en cada ciclo reproductivo aparentemente fue exitosa, a excepción de los años con perturbaciones ambientales en la que no hubo reproducción, pero después de concluída la reproducción los polluelos no llegan a sobrevivir al año de edad, produciéndose altos porcentajes de mortalidad por la escasez de alimento (principalmente anchoveta). Estas mortalidades ocurrieron en 13 años no consecutivos, con porcentajes de 70 a 100% de mortalidad de polluelos; razón por la que el nivel poblacional de guanay se mantiene bajo.

Incremento y mortalidad de piquero (Tabla 8, Fig. 8):

En la década del 60, los mayores incrementos de la población de piquero se produjeron en 1964/65, 1966/67 y 1968/69 con 32, 30 y 48%, respectivamente; pero también se produjeron mortalidades, notándose las más altas mortalidades de adultos en 1962/63, 1963/64, 1965/66 y 1967/68 con 8, 23, 64 y 10%, respectivamente; y la mortalidad de polluelos fueron muy altas llegando al 100% a excepción de los años en que se produjeron incrementos.

Durante la década del 70 se produjo incrementos superiores al 35% en los ciclos reproductivos 1973/74, 1975/76, 1977/78 y 1978/79, además hubo incrementos de 8 y 15% en 1970/71 y 1971/72, respectivamente. La mortalidad más alta ocurrió en 1972/73 con 55% de la población total y con 7, 9, 19 y 4% para los años 1974/75, 1976/77, 1979/80 y 1980/81, respectivamente.

En la década del 70 las mortalidades de los polluelos también fueron muy altas, a excepción de los años en que se produjeron incrementos, durante los cuales se observa cero de mortalidad.

Incremento y mortalidad de alcatraz o pelícano (Tabla 9, Fig. 8):

De las tres especies principales de aves guaneras, el alcatraz o pelícano fue la única especie que no fue afectada en forma duradera por los fenómenos ambientales y los altos volúmenes de captura de anchoveta para la industria. Después de cada descenso poblacional causado por los cambios ambientales, ésta se recuperó rápidamente, como lo demuestran los altos porcentajes de incrementos que inclusive en algunos casos como en 1973/74 y 1978/79 llegaran a 105 y 107%, respectivamente.

La mortalidad de adultos fue alta en los ciclos reproductivos de 1963/64 y 1972/73 con 71 y 63%, respectivamente. En cambio, la mortalidad de polluelos fue alta en la mayoría de los años, lo que demostraría que la población adulta se mantuvo en fluctuación pero siempre con un ritmo ascendente, superando en forma amplia los niveles poblacionales de la década del 60.

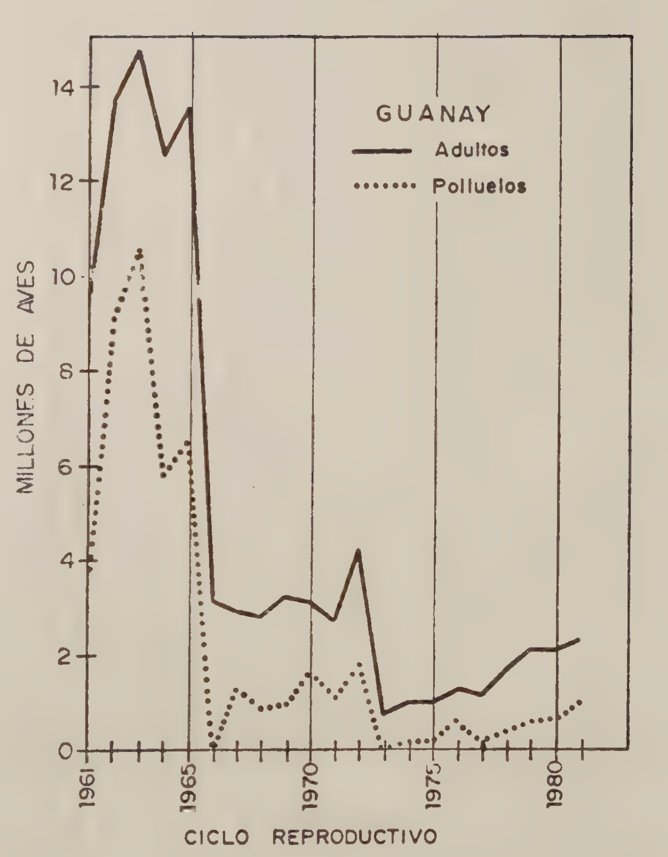


Fig. 5.- Guanayes adultos y polluelos en cada ciclo reproductivo.

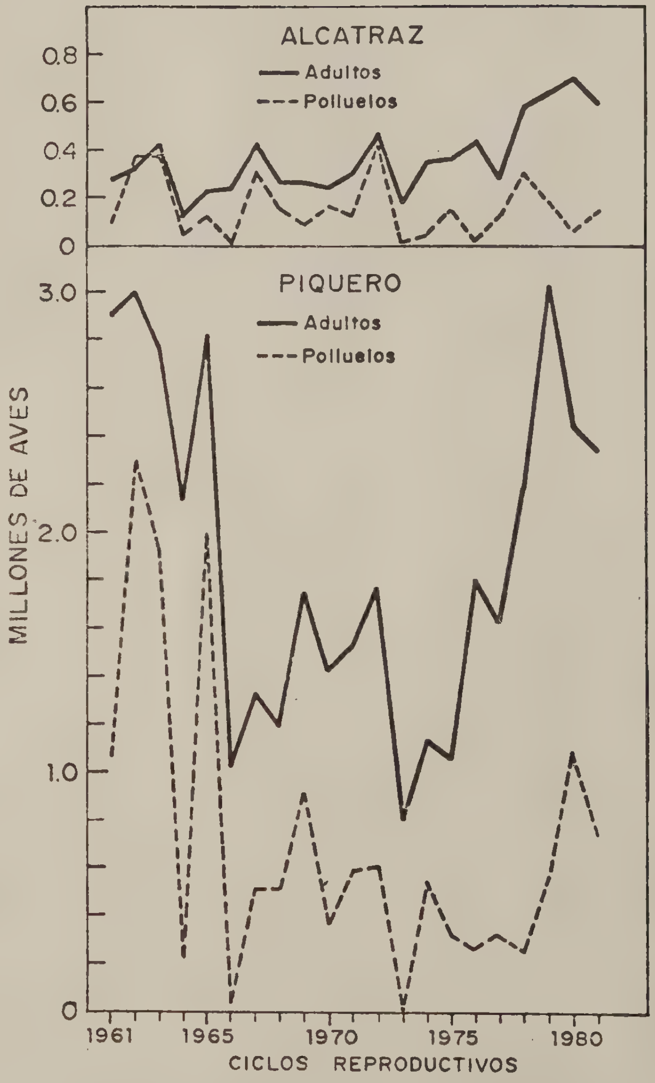


Fig. 6.- Población de Alcatraz y Piquero adulto y polluelos en cada ciclo reproductivo.

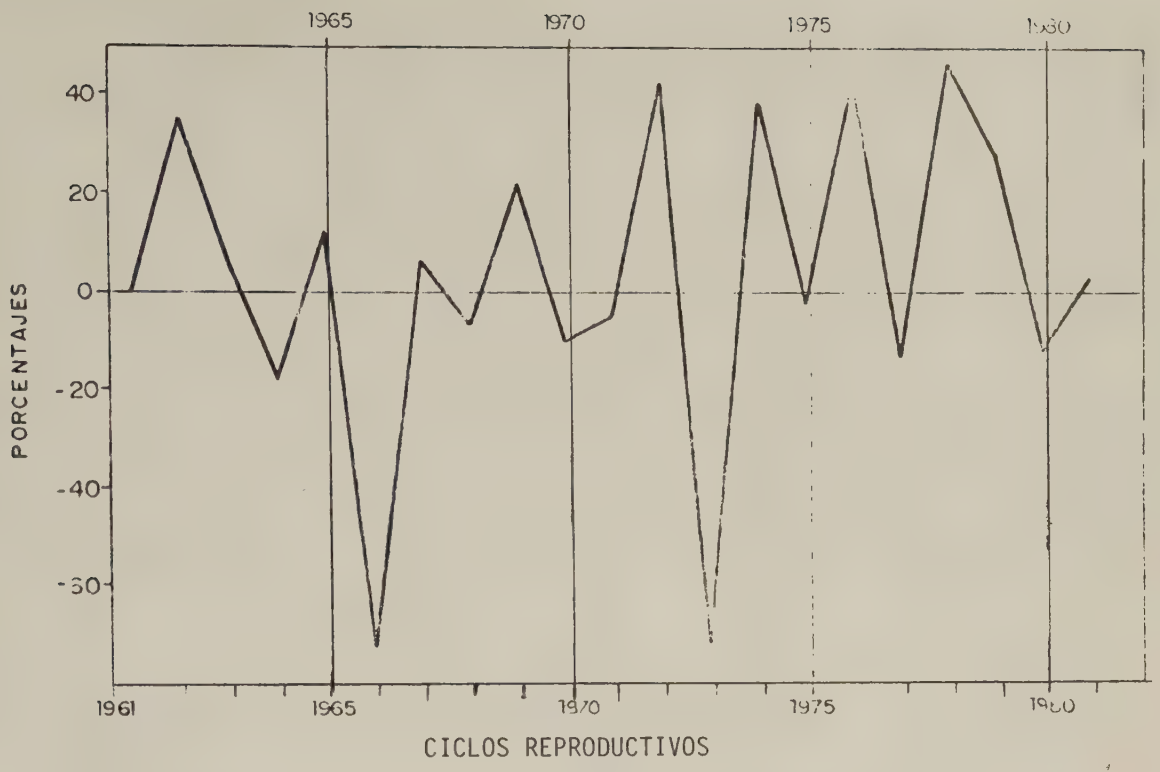


Fig. 7.- Incremento y Mortalidad de la población de aves guaneras.

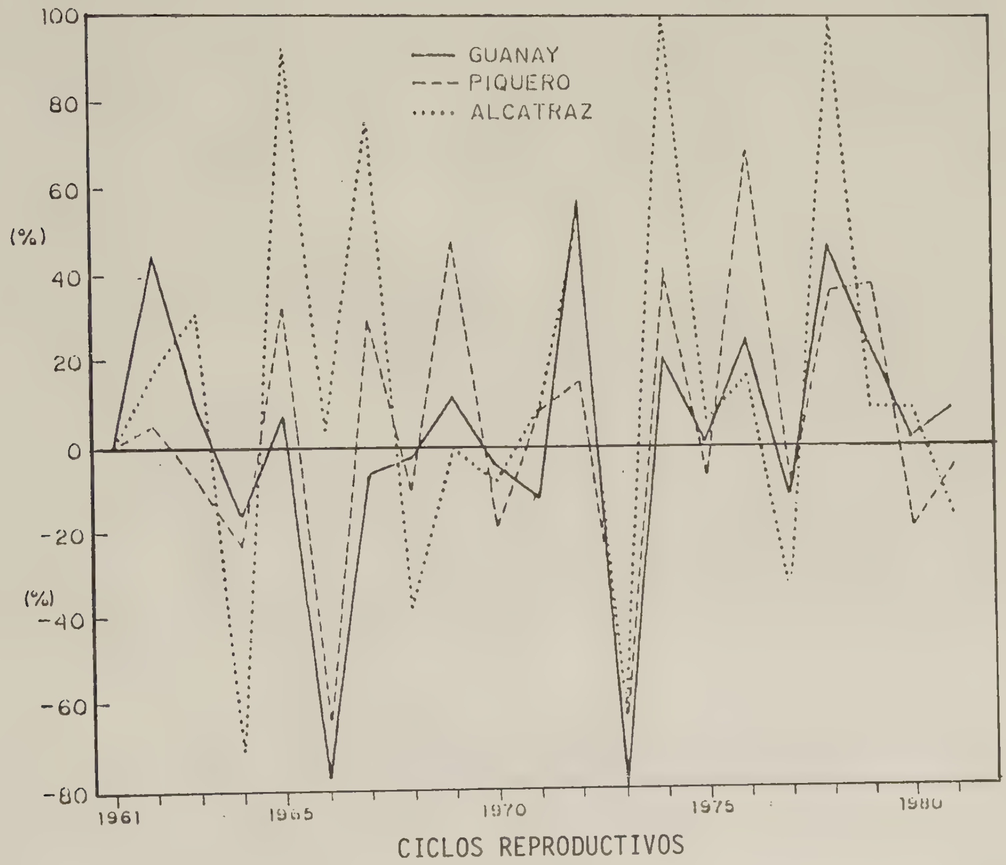


Fig. 8.- Incremento y mortalidad por especies en (%)

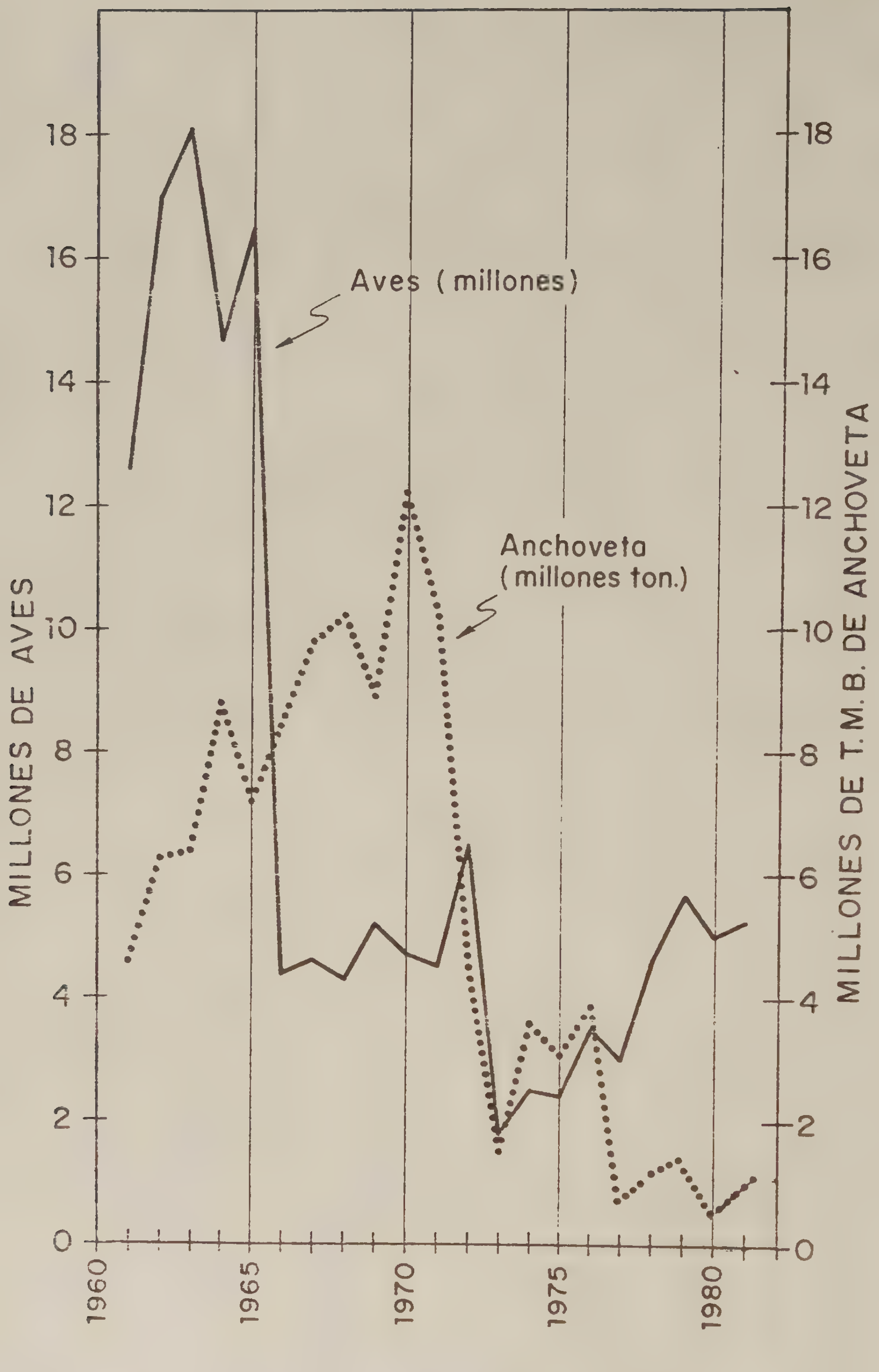


Fig. 9.- Población de aves guaneras (millones de individuos) y monto total de captura de anchoveta (en millones de ton.).

LAS AVES Y LA DISPONIBILIDAD DE ANCHOVETA

El recurso anchoveta desempeñó un papel muy importante en el desarrollo de poblaciones de aves por constituir la anchoveta el principal alimento de estas aves. Por esta razón, la mayor o menor disponibilidad del recurso anchoveta influyó directamente en las fluctuaciones de los niveles poblacionales de las aves.

De las estadísticas de captura anual de anchoveta se puede deducir que en la década del 60 aumentó la porción de este recurso tomada por la pesquería, no así la tomada por las aves que comenzaron a descender de 18 millones en 1963 hasta 4.31 millones de aves en 1968; por el contrario, la captura anual de anchoveta llegó a su máximo en 1970 con más de 12 millones de TMB.

En la década del 70, a consecuencia de las anomalías del medio ambiente marino ocurrido en 1972/73 y la sobrepesca de anchoveta en la década del 60 y comienzos del 70, la disponibilidad de anchoveta para alimento de las aves e inclusive para la pesquería, fue escasa. Al respecto Tsukayama (en prensa) hace una descripción secuencial de la pesquería de la anchoveta en el Perú. Aduciendo que en los últimos años el recurso anchoveta ha sido reemplazado por otros recursos ícticos. Jordán, Csirke y Tsukayama (1978) opinan que frente a la escasez de anchoveta se produjeron fenómenos de compensación, o sea, incremento de otros recursos.

CONCLUSIONES

Se han analizado datos de censos gráficos de las poblaciones de aves guaneras, con particular énfasis en los ciclos reproductivos 1974/75 - 1980/81.

En este período de la población de aves varió de 2.46 a 5.21 millones de aves notándose una lenta recuperación del nivel poblacional; sin embargo, la pesquería y los trastornos ambientales marinos siguen siendo factores limitantes en el desarrollo de poblaciones de aves guaneras.

En cuanto a la composición por especies, el piquero (*Sula variegata*) sigue predominando sobre el guanay (*Phalacrocoraz bougainvillii*) y pelícano o alcatraz (*Pelecanus thagus*).

El recurso anchoveta sigue siendo escaso para alimento de las aves e inclusive para la pesquería industrial.

En la década del 70, la población más alta fue 6.47 millones en 1971/72 contituido por 66, 27 y 7% de guanay, piquero y alcatraz o pelícano, respectivamente. El nivel más bajo de 1.81 millones se observó durante el Fenómeno "El Niño" de 1972, donde se observaron porcentajes de 46, 44 y 9% de guanay, piquero y alcatraz, respectivamente. En los siguientes años se nota una lenta recuperación, llegando a 1980/81 con 5.21 millones de aves, compuesta por 45, 44 y 11% de piquero, guanay y alcatraz o pelícano, respectivamente.

Estos dos principales factores arriba citados, además de causar descensos en el nivel poblacional, han ocasionado considerables cambios en la composición por especies.

En el descenso poblacional, la especie guanay fue la más afectada; en cambio, el piquero y alcatraz han recuperado prácticamente su nivel poblacional, porque el problema de la escasez o poca disponibilidad de anchoveta para estas dos últimas especies fue solucionado cambiando la alimentación hacia otras especies ícticas.

AGRADECIMIENTOS

Expreso mi más sincero agradecimiento a la Biólogo Isabel Tsukayama por el interés demostrado en la elaboración del presente trabajo y las acertadas sugerencias; de la misma forma agradezo a Pesca Perú Fertilizantes (antes Servicio Nacional de Fertilizantes), especialmente al Dr. Demóstenes Cabrera por las facilidades brindadas en la obtención de información de los censos gráficos de aves guaneras y al personal de la Unidad de Dibujo por la preparación de las figuras. Finalmente, agradezo a la Sra. Isabel Delgado de Risso por el mecanografiado del manuscrito original de este trabajo.

REFERENCIAS

Avila, E. 1954. Potencial deyectiva del guanay (Ph. bougainvillii). Bol.Cient.Cia.Admora.Guano. 1(2):22-49.

Compañía Administradora del Guano. 1946. 37a Memoria del directorio de la Compañía Administradora del Guano, correspondiente al año económico de 1945.

____________. 1954. El guano. Cia.Admora.Guano. 1-30.

____________. 1955. 47a Memoria del directorio correspondiente al ejercicio 1955.

Corporación Nacional de Fertilizantes. 1964. Memoria de la Corporación Nacional de Fertilizantes correspondiente al año 1964.

Fuentes, H. 1969. Las poblaciones de las aves guaneras después de 1965. Serie de Informes Especiales Inst.Mar Perú-Callao. IM-54:1-18.

Gamarra, D.L. 1955. Ensayo sobre la zoonomía de la aves guaneras del Perú. Bol.Cia.Admora.Guano II:73-121.

____________. 1964a. Las fluctuaciones en la población de las aves guaneras en la costa peruana. Bol.Cia.Admora.Guano. 2(12) 2 Epoca:3-12.

____________. 1964b. Las fluctuaciones de la población de palmípedas marinas productoras del guano del Perú. Memoria de Fertilizantes correspondiente al año 1964.

Jordán, R. 1963. Resultados de los censos gráficos de las aves guaneras efectuados en noviembre de 1960 y enero de 1962. Callao, Inf.Inst.Recurs.Mar. 12:1-21.

____________. 1964. Las emigraciones y mortalidad de las aves en invierno y otoño de 1963. Callao, Inf.Inst.Invest.Recurs.Mar. 27:1-31.

Jordán, R. y H. Fuentes. 1964. Resultados de los censos gráficos de las aves guaneras efectuados durante el ciclo reproductivo 1962/63. Callao, Inf.Inst.Invest.Recurs.Mar. 22:1-15.

____________. 1966. Las poblaciones de aves guaneras y su situación actual. Informe Inst.Mar Perú-Callao. 10:1-44.

Jordán, R., J. Csirke y I. Tsukayama. 1978. Situación de los recursos anchoveta, sardina, jurel y caballa a junio de 1978. Informe Inst.Mar Perú-Callao. 56:1-32.

Murphy, R.C. 1954. El guano y la pesca de anchoveta. Cia.Admora.Guano. Informe Oficial al Supremo Gobierno. 1-39.

Tovar, H. 1978. Las poblaciones de aves guaneras en los ciclos reproductivos de 1969/70 a 1973/74. Informe Inst.Mar Perú-Callao. 45:1-13.

Tovar, H. y L. García. 1982. Las poblaciones de aves guaneras durante "El Niño" de 1957. Boletín de Lima. 22:34-46, año 4 de julio de 1982.

Tovar, H. y N. Galarza. (En prensa). Cambios en el régimen alimentario de guanay (Phalacrocorax bougainvillii lesson).

____________. (En prensa). Fluctuaciones mensuales de las poblaciones de aves guaneras durante "El Niño" de 1972.

Tsukayama, I. (En prensa). Recursos pelágicos y sus pesquerías en el Perú.

Vogt, W. 1942. Informe sobre las aves guaneras. Bol.Cia.Admora.Guano. II(8):9-28.

____________. 1942. Informe sobre las aves guaneras. Bol.Cia.Admora.Guano. II(9):6-48.

____________. 1942. Informe sobre las aves guaneras. Bol.Cia.Admora.Guano. II(10):5-40.

BATCH FECUNDITY AND SPAWNING FREQUENCY OF VARIOUS ANCHOVY (Genus: *Engraulis*) POPULATIONS FROM UPWELLING AREAS AND THEIR USE FOR SPAWNING BIOMASS ESTIMATES*

by

J. Alheit,[1] B. Alegre,[2] V.H. Alarcōn,[2]
and B. Macewicz[3]

[1] Programa Cooperativo Peruano-Alemān de Investigaciōn Pesquera (PROCOPA), IMARPE, Apartado 22, Callao, Perū

[2] Instituto del Mar del Perū, Apartado 22, Callao, Perū

[3] Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, U.S.A.

* Publication No. 7 of PROCOPA

Resumen

Recientemente se han revelado varias características esenciales de la biología reproductiva de la anchoveta peruana (*Engraulis ringens*) y ahora pueden ser comparadas con aquellas de la anchoveta del norte (*E. mordax*). Así como la anchoveta del norte, la anchoveta de sistema de afloramientos de Perú desova en forma parcial, depositando varias series de huevos a lo largo del año. Ahora se dispone de datos de series de tiempo sobre la fecundidad parcial de varias sub-poblaciones de ambas especies. La variabilidad de la fecundidad parcial es alta dentro de cada año y de un año a otro. En ambas especies, la fecundidad parcial aumenta a medida que aumenta la latitud. Fuera de las épocas principales de desove (Agosto-Septiembre y Enero) la fecundidad parcial de la anchoveta peruana disminuye. Durante El Niño de 1976, la fecundidad parcial de *E. ringes* disminuyó considerablemente. Esto se atribuye a las condiciones desfavorables de alimentación. La fecundidad parcial de *E. capensis* frente al sudoeste de Africa se encuentra dentro del rango de los valores de las otras dos especies. La frecuencia del desove fue determinada por exámenes histólogicos de los ovarios para observar la incidencia de folículos post-ovulatorios. La fracción de hembras maduras que desovan por día fue de 16% en 1961 frente a Perú y 14.5% en 1980 frente a California. Todos los parámetros reproductivos investigados son muy similares en ambas especies, indicando una relación filogénetica estrecha. La importancia de determinar la fecundidad parcial y la frecuencia del desove se basa en su uso para "el método de la producción de huevos" que fue desarrollado recientemente para estimar la biomasa desovante de anchoveta. Este método ha sido aplicado con suceso en los stocks de anchovetas frente a California y Perú. Se discuten los resultados, ventajas y futuras aplicaciones de este método para otras especies de peces pelágicos que forman cardúmenes tales como sardinas.

INTRODUCTION

Recently, a new method, the 'Egg Production Method', was developed by the Southwest Fisheries Center, California, to estimate the spawning biomass of anchovies (Parker, 1980; Stauffer and Picquelle, 1980). This method requires the determination of reproductive parameters like batch fecundity and spawning frequency, i.e. the fraction of mature females spawning per day.

The determination of batch fecundity and spawning frequency for multiple spawning pelagic fish, like the anchovy, posed several problems which were solved by Hunter and Goldberg (1980). In traditional methods, size - frequency diagrams of oocytes were established and it was assumed that fecundity could be determined by counting the number of all oocytes contained in the most advanced mode. Hunter and Goldberg (1980) discussed the problems involved in this method. Instead, they determined the batch fecundity by counting the number of hydrated oocytes in the ovaries. This method takes much less time and yields a higher precision than traditional methods. For the determination of the spawning frequency, Hunter and Goldberg (1980) used the incidence of postovulatory follicles in anchovies. They were able to age postovulatory follicles and to determine the day when a particular female had spawned. All these studies were carried out on the northern anchovy (*Engraulis mordax*). Recently, the same methods were applied successfully, to the Peruvian anchovy (*E. ringens*) (Alheit el al., in prep.; Santander et al., in prep.).

Time series are available now on the batch fecundity of the Peruvian and the northern anchovy. The data were partly gained from previous studies using traditional methods (MacGregor, 1968; Laroche and Richardson, 1980) and from samples collected in Peru during the seventies which were processed recently.

The objectives of this study are (1) to compare the time series on batch fecundity of the two anchovy species, (2) to compare for both species the data on batch fecundity and spawning frequency gained by the new methods, and (3) to discuss their use for estimates of spawning biomass of multiple spawning pelagic fish.

This study was a cooperative effort of the Southwest Fisheries Center, California, the Instituto del Mar del Peru and the Peruvian-German Fisheries Research Project (PROCOPA) which is financed by the German Agency of Technical Cooperation (GTZ).

METHODS

The batch fecundity of the Peruvian anchovy samples collected in the seventies was determined by macerating the connective tissue of the ovaries in Gilson's fluid (Simpson, 1951), a process which releases the oocytes. The size of the oocytes was measured and the number of oocytes in the most advanced mode was determined by means of probability paper (Cassie, 1954). The recent batch fecundity data for the Peruvian and northern anchovy were gained by using hydrated oocytes (Hunter and Goldberg, 1980). The methods used for determining the batch fecundity of other anchovy populations presented here are described in MacGregor (1968) for the northern anchovy in 1951-60, in Laroche and Richardson (1980) for the northern population of the northern anchovy and in LeClus (1979) for the anchovy off South West Africa (*E. capensis*). The spawning frequency was determined according to the methods described by Hunter and Goldberg (1980), Stauffer and Picquelle (1980) and Alheit et al. (in prep.).

Table 1: Mean number of oocytes per gram ovary, mean number of oocytes per gram female and geometric mean regression (Ricker, 1973) of eggs per spawn (= batch fecundity) on gonad-free female wet weight.

[illegible]	Species	Sub-population	Year	Month	Sample Size	Size Range of fish (gonad-free weight in g)	Mean Nr Oocytes per g female	S.D.	Mean Nr. Oocytes per g Ovary	S.D.	r	Slope	Y-intercept
1	E. ringens	central	1970	Jan	19	15.2 - 40.0	7 123	± 2719	375	± 147	.685	1 048	-16 627
2	" "	"	1973	Sep	26	15.1 - 38.7	5 998	± 2728	410	± 172	.564	746	- 8 527
3	" "	"	1974	Jan	8	22.8 - 43.2	9 231	± 1938	489	± 133	.554	847	-13 125
4	" "	"	"	Feb	8	32.2 - 44.2	6 011	± 999	326	± 91	.126	667	-13 506
5	" "	"	"	Aug	12	17.7 - 41.3	7 067	± 2049	484	± 157	.717	1 517	-31 194
6	" "	"	"	Sep	9	21.0 - 48.4	8 233	± 1577	410	± 142	.692	705	- 8 814
7	" "	"	"	Oct	18	16.3 - 54.5	6 607	± 2295	268	± 110	.799	558	- 8 804
8	" "	"	1976	Aug	32	6.8 - 34.5	11 606	± 5447	415	± 143	.813	424	- 227
9	" "	"	"	"	11	15.0 - 34.5	7 686	± 1800	414	± 149	.509	360	1 257
10	" "	southern	1973	Sep	19	14.1 - 21.7	7 205	± 3125	395	± 122	.614	1 352	-17 490
11	" "	"	1974	Aug	23	9.0 - 41.3	6 432	± 2351	446	± 175	.831	1 087	-13 545
12	" "	northern + central	1981	Aug/ Sep	437	15.0 - 38.0	*)		580	± 139	.806	981	-10 279
13	E. ringens	central	1981	Aug/ Sep	254	15.0 - 38.0	*)		637	± 134	.769	1 213	-14 745
14	" "	northern	"	Aug/ Sep	183	15.0 - 38.0	*)		502	± 103	.883	824	- 7 655
15	E. mordax[1)]	central	1951-1960		19	9.3 - 32.1	12 253	± 2737	606	± 151	.795	670	- 1 247
16	" "	"	1978		23	9.3 - 31.9	*)		389	± 141	.511	528	- 2 790
17	" "	"	1979		44	9.3 - 28.1	*)		438	± 150	.784	881	- 7 917
18	" "	"	1980		33	17.11+)	*)		444	± 80	.903	624	- 2 933
19	" "	"	1981		127	14.75+)	*)		601	± 180	.873	872	- 3 711
20	" "	"	1982		109	16.54+)	*)		606	± 151	.724	852	- 4 061
21	" "	northern[2)]	1977		17	14.4 - 31.3	7 137	± 3997	869	± 213	.860	1 494	-12 015
22	E.capensis[3)]		1977		14	17.5 - 24.3	4 491	± 851	644	± 153	.451	1 542	-18 657

1) From MacGregor (1968) 2) From LaRoche and Richardson (1980) 3) From LeClus (1979)
*) Parameter not calculated as hydrated oocytes were used +) Average weight

RESULTS

Time series on fecundity of Peruvian anchovy. 14 different data sets on fecundity of the Peruvian anchovy are available (Table 1). They originate from different years, months and areas. There are no trends recognizable for the mean number of oocytes per gram female, however, some interesting features can be pointed out. Only one data set, January 1970, was collected before the crash of the Peruvian anchovy in 1972. This value is relatively, but not particularly low. The data set from August 1976 was collected during an 'El Niño' year. The collection includes many very small mature females between 7 and 15 g. To make this data more comparable, another data set comprising only the larger specimens (11 fish) is presented separately. The values from August 1976 lie just within the range of the other data sets. There are two data sets from the south, but they are not outliers. The only remarkable feature is the difference between the relatively low values from the seventies and the high values from 1981. This difference is probably not caused by the use of different methods. In 1981, two data sets were taken, one from the central region and one from the northern region. The one from the central region is with 637 eggs per gram female; much higher than the 499 eggs per gram female from the northern region. This might not necessarily be a regional difference, as the northern samples were, on average, collected two weeks later than the central samples. It could be that the value for the number of eggs per gram female is very flexible and can change very fast towards the end of the spawning season. In general, one can observe a decrease of the mean number of eggs per gram female after the main spawning periods in August/September and January, e.g. in 1974 and 1981. The number of oocytes per gram ovary, does not show any trend. Only the value for the large data set from August 1976 lies outside of the range of the other values. However, this high value is caused, solely, by the high number of very small mature females. The mean number of oocytes per gram ovary is not given for 1981, as this value changes during the process of hydration.

The relationship between batch fecundity and female weight (ovary-free) was investigated further by using the geometric mean regression (Ricker, 1973). Whereas all other data from the Peruvian anchovy have a relatively high Y - intercept, only the data from August 1976 have a positive and a relatively low negative value (Table 1). Differences between the 14 data sets become more obvious from the regression lines in Figures 1-3. They are presented in three different groups whereby the whole data set from August 1981 serves as a reference line. Group 1 includes all the data collected during the yearly peak spawning periods in August/September and January (Figure 1). These regression lines are not too different from each other. The second group comprises the 'El Niño' data from August 1976 and data sets collected at February 1974 and October 1974, outside of the yearly main spawning periods (Figure 2). These data sets have in common a relatively low batch fecundity for females larger than 30 g. The third group demonstrates regional differences. Obviously the fecundity values from the southern Peruvian anchovy stock are higher than in the central and northern stock. Although the data sets were taken in

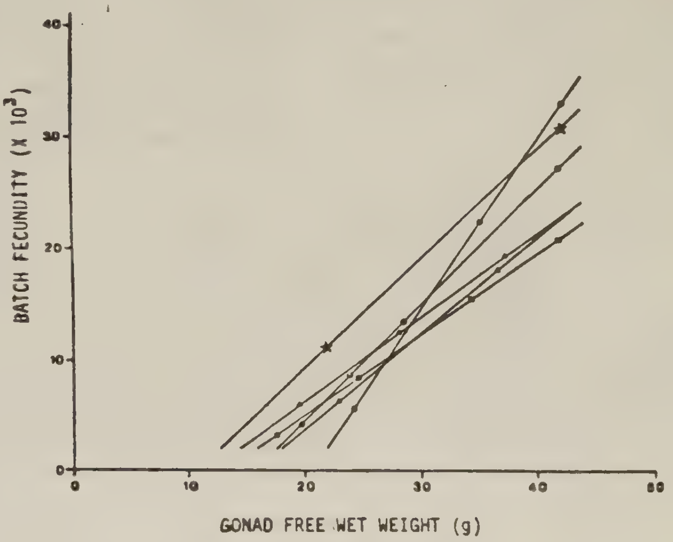


Fig. 1. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
○ = Lot 1
● = Lot 11
▲ = Lot 2
△ = Lot 3
■ = Lot 6

different years, they indicate, that the batch fecundity increases with increasing latitude (Figure 3).

Comparison of fecundity of different anchovy species. Batch fecundity data are available for the Peruvian anchovy, the northern anchovy and the anchovy from South West Africa. The values for the mean number of oocytes per gram female from the northern anchovy and the anchovy off South West Africa lie within the range of the Peruvian data (Table 1). The only exception is the high value for the northern population of the northern anchovy. From 1978 to 1982 the values of the central population of the northern anchovy increased steadily from 389 to 606 eggs per gram female weight.

The regression lines of the central population of the northern anchovy are relatively uniform (Figure 4). However, the regression line of the northern population is very distinct and demonstrates that females with more than 15 g weight have a much higher batch fecundity than in the central population. Again, as in Peru, the batch fecundity of anchovy populations increases with increasing latitude.

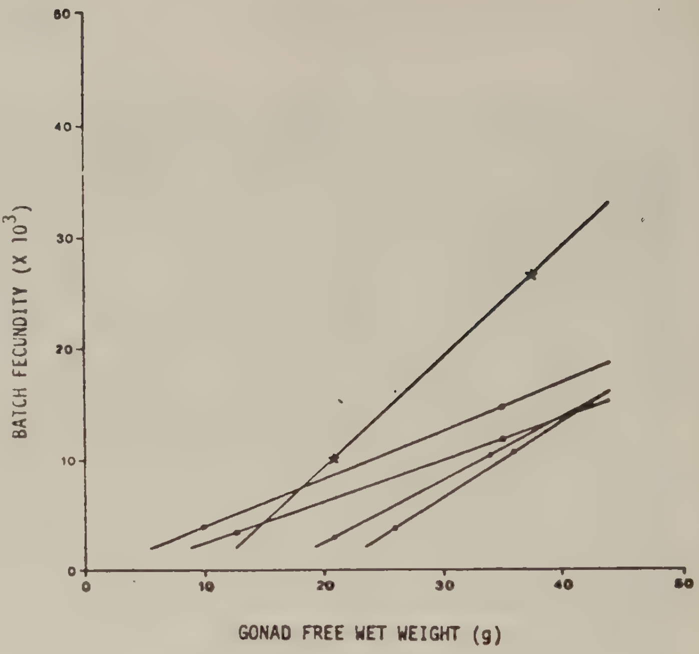
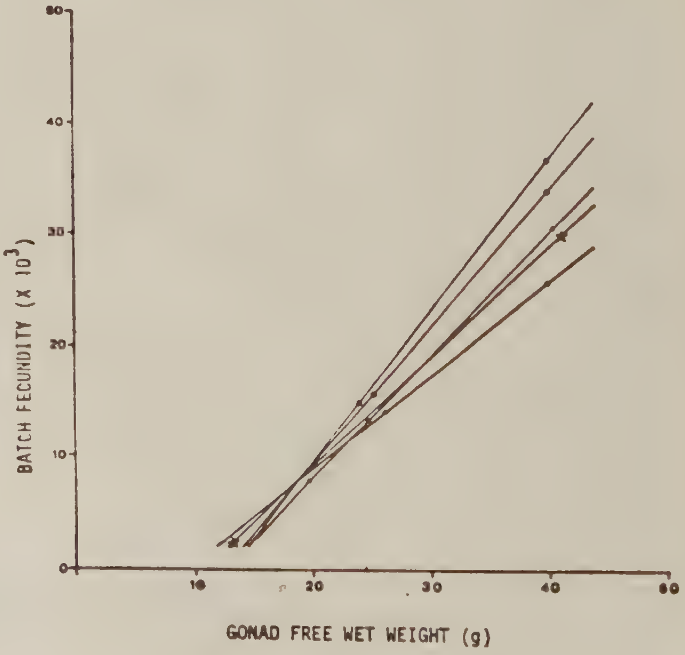


Fig. 2. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 8
▲ = Lot 7
○ = Lot 8 (only females >12 g).
△ = Lot 4

Fig. 3. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 10
▲ = Lot 11
○ = Lot 13
△ = Lot 4



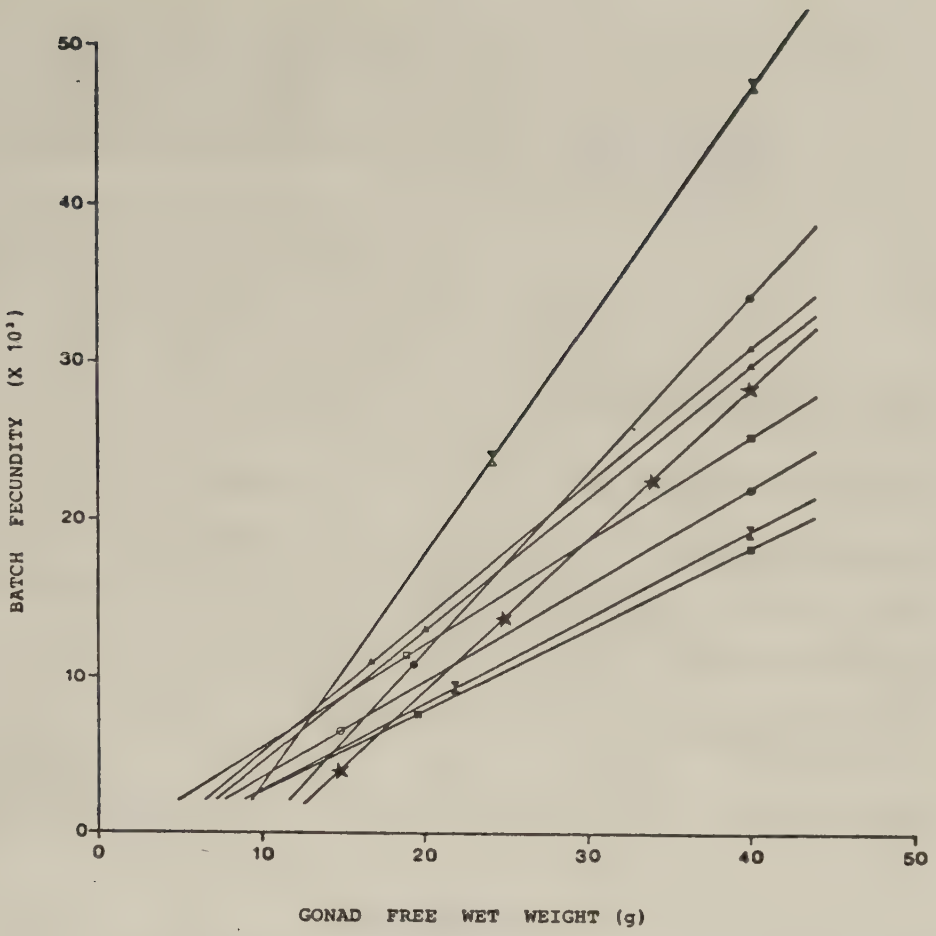


Fig. 4. Comparison of Different Species. Batch fecundity of anchovy populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14 *E. ringens*
● = Lot 17 *E. mordax*
▲ = Lot 20 *E. mordax*
○ = Lot 18 *E. mordax*
⧗ = Lot 22 *E. capensis*

⧖ = Lot 21 *E. mordax*
△ = Lot 19 *E. mordax*
□ = Lot 15 *E. mordax*
■ = Lot 16 *E. mordax*, 1978, central population

Spawning frequency. The fraction of mature females spawning per day was determined for the Peruvian anchovy in August/September 1981. As a purse seiner was used to collect the adult anchovies, fish samples could be obtained at any time of the day and two data sets were established, one giving the fraction of females which spawned one day before being collected and the other one giving the fraction of females which had spawned two days before being sampled. These two spawning fractions were 17.26% and 14.81%, respectively (Alheit el al., in prep.).

The agreement of these two data sets demonstrates the validity of the method introduced by Hunter and Goldberg (1980). The spawning frequency determined for the Peruvian anchovy by combining these two data sets was 16.04%. That means every day during August/September 1981, on average, 16.04% of the mature females were spawning, or in other words, a female of the central and northern Peruvian stock spawned, on average, every 6.2 days a new batch of eggs. The spawning frequency recorded for the northern anchovy in 1981 was 14.5% (Stauffer and Picquelle, 1980) a value very similar to that one of the Peruvian anchovy.

Use of data on reproductive biology for estimates of spawning biomass. Batch fecundity and spawning frequency are two of the five parameters used for determining the spawning biomass of anchovies by means of the 'Egg Production Method' (Parker, 1980; Stauffer and Picquelle, 1980). So far, this method has been applied in California and Peru. The results of the Californian survey from 1980 (Stauffer and Picquelle, 1980) and from the Peruvian survey from 1981 (Santander et al., in prep.) are listed in Table 2.

Table 2: Results of spawning biomass estimates gained by application of 'Egg Production Method' in Peru 1981 and California 1980. Parameter estimates ($\hat{x}$) and estimates of spawning biomass with associated coefficient of variation ($CV_{\hat{x}}$). The data for Peru comes from Santander et al. (in prep.) and for California from Stauffer and Picquelle (1980).

	Peru 1981		California 1980	
	$\hat{x}$	$CV_{\hat{x}}$	$\hat{x}$	$CV_{\hat{x}}$
Daily egg production in survey area	$6.985.10^3$	0.2586	(10.50)*	0.103
Average female weight (g)	25.84	0.0259	17.50	0.0547
Fraction of females	0.564	0.0459	0.476	0.120
Batch fecundity (eggs/female)	15 401	0.0427	7 788	0.0749
Spawning frequency	0.160	0.0588	0.145	0.125
Spawning biomass (million tons)	1.295	0.2739	0.859	0.225

* This value is the number of eggs per ton.

DISCUSSION

The comparison of the batch fecundity data of different anchovy populations demonstrates clearly the high plasticity in batch fecundity of anchovies. There is a high variability in batch fecundity within years and between years as the Peruvian and Californian data show. One can only speculate about what causes this variability. Sufficient quantities of the right food are probably a very important condition for a fish to build up a high batch fecundity as argued by Bagenal (1978) and Wootton (1979). This might be indicated by the low fecundity values during the 'El Niño' year 1976 when feeding conditions were unfavourable for the Peruvian anchovy.

Tsukayama and Alvarez (1980) reported that during the 'El Niño' 1976 growth of the Peruvian anchovy was retarded and that the mean size of mature females was considerably less than in normal years. They suggested that the high proportion of small females would reduce the fecundity of the whole population. This hypothesis is confirmed by the data presented here. Population fecundity in 1976 was further reduced by the much lowered fecundity values of the larger females in comparison to other years (Figure 2). This lowered population fecundity is caused by the combined effect of a high proportion of small females and of large females having a lower batch fecundity than in normal years and certainly exerted a negative influence on subsequent recruitment.

The importance of the determination of batch fecundity and spawning frequency is based on their applications in the 'Egg Production Method' to estimate the spawning biomass of anchovies. The main advantages of the 'Egg Production Method' are its high precision and that it needs relatively little ship time. It consists of 5 biological parameters and error estimates can be determined for each of them (Table 2). To date, it has been applied four times in the Californian upwelling system (1980-1983) and once in Peru (1981).

Up to now, it was applied only to anchovies. However, it is suitable for other multiple spawning pelagic fish species, too. Recently, postovulatory follicles have been identified and aged for the Peruvian sardine (*Sardinops sagax sagax*) (Alarcon et al., in prep.), a vital step towards the application of the 'Egg Production Method' for sardines.

REFERENCES

Alarcón, V.H., S.R. Goldberg and J. Alheit. (In preparation). Histología de folículos post-ovulatorios de la sardina, Sardinops sagax sagax, del Perú. Bol.Inst.Mar Perú, Callao.

Alheit, J., V.H. Alarcón and B.J. Macewicz. (In preparation). Spawning frequency and sex ratio in the Peruvian anchovy, Engraulis ringens.

Bagenal, T.B. 1978. Aspects of fish fecundity. In Ecology of Freshwater Fish Production (S.D. Gerking, ed.). Blackwell Scientific Publications, Oxford. 520 p.

Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Aust.J.Mar.Freshwater Res. 5:513-522.

Hunter, J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish.Bull.U.S. 77:641-652.

Laroche, J.L. and S.L. Richardson. 1980. Reproduction of northern anchovy, Engraulis mordax, off Oregon and Washington. Fish.Bull.U.S. 78:603-618.

Le Clus, F. 1979. Fecundity and maturity of anchovy Engraulis capensis off South West Africa. Fish.Bull.S.Afr. 11:26-38.

MacGregor, J.S. 1968. Fecundity of the northern anchovy, Engraulis mordax Girard. Calif.Fish Game. 54:281-288.

Parker, K. 1980. A direct method for estimating norhtern anchovy, Engraulis mordax, spawning biomass. Fish.Bull.U.S. 78:541-544.

Ricker, W.E. 1973. Linear regression in fishery research. J.Fish.Res.Board Can. 30:409-434.

Santander, H., J. Alheit and P.E. Smith. (In preparation). Estimación de la biomasa desovante de la anchoveta Peruana, Engraulis ringens, del stock central y norte en 1981 usando el "Método de Producción de Huevos". Bol.Inst.Mar Perú, Callao.

Simpson, A.C. 1951. The fecundity of the plaice. Fishery Invest., Lond., Ser. 2. 17:27 p.

Stauffer, G.D. and S.J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Southwest Fisheries Center Adminsitrative Rep. No. LJ-80-90.

Tsukayama, I. and M.A. Alvarez. 1981. Fluctaciones en el stock de anchovetas desovantes durante las temporadas reproductivas de primavera 1964-1978. Bol.Inst.Mar Perú, Callao. Volumen extraordinario:50-54.

Wootton, R.J. 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. pp. 133-159. In Fish Phenology: anabolic adaptiveness in teleosts (P.J. Miller, ed.). Academic Press, London. 443 p.

ON THE SEASONAL GROWTH, MONTHLY RECRUITMENT AND MONTHLY BIOMASS OF PERUVIAN ANCHOVETA (*Engraulis ringens*) FROM 1961 TO 1979*

by

D. Pauly[1] and I. Tsukayama[2]

[1] International Center for Living Aquatic Resources Management
(ICLARM), MCC P.O. Box 1501, Makate, Metro Manila, Philippines

[2] Instituto del Mar del Perū, Apartado Postal 22, Callao, Perū

* ICLARM Contribution No. 145, PROCOPA Contribution No. 14.

Resumen

Se han examinado en detalle datos de longitud-captura mensual de anchoveta peruana (*Engraulis ringens*) correspondientes a la región Norte, usando los programas de computadora ELEFAN I y III (Electronic LEngth Frequency ANalysis). ELEFAN I proporcionó para cada uno de los años, desde 1961 a 1979, valores similares de L_∞ y K de la ecuación de crecimiento de Von Bertalanffy. Se muestra que ocurren oscilaciones estacionales en el crecimiento, los cuales son cuantificados.

El programa ELEFAN III, que permite la aplicación de diferentes formas del análisis de población virtual en base a datos de longitud-captura, fue empleado para obtener series de tiempo, sobre una base mensual, de los siguientes parámetros: reclutamiento (R), stock desovante (S) y biomasa total (B). También se presentan y discuten series de tiempo de capturas mensuales (C) y de valores derivados ($\log_e$ (R/S) y F = C/B).

INTRODUCTION

For about 10 years (1962-1971), the Peruvian anchoveta (*Engraulis ringens*, Jenyns [Fam: Engraulidae]) supported the largest single-species fishery in the world, with annual catches in excess of 12 million tonnes. Present catches are lower, but still make this species a very important aquatic resource (see contributions in Glantz and Thompson, 1981). The anchoveta has been much studied, and indeed, most methods available for assessing exploited fish stocks have been applied to the anchoveta, often by the very scientists who developed these methods (Boerema et al., 1967; Schaefer, 1967; Gulland, 1968; IMARPE, 1970, 1972, 1973, 1974, 1977a).

The present paper continues this tradition in that it reports on the application to the anchoveta of a newly developed set of methods for the investigation of exploited fish stocks. The set of methods are incorporated in the ELEFAN (Electronic LEngth Frequency ANalysis) programs developed at ICLARM*, which are applied to catch-at-length data from the Northern Region of Peru and covering the years 1961 to 1979.

Of the three available, the two ELEFAN programs used were:

- ELEFAN I (Pauly and David, 1981; Pauly et al., 1980); this program is used for the extraction of growth parameters from length-frequency (L/F) or catch-at-length (C/L) data, using an algorithm which allows for seasonal growth oscillations to be considered and which provides results that are fully reproducible.
- ELEFAN III (Pope et al., MS, cited in Pauly, 1982); this program was used to run two types of length-structured virtual population analysis (VPA) on catch-at-length data, and to obtain estimates of recruitment, standing stock and fishing mortality on a monthly basis.

The analyses performed and the conclusion reached here are, for reasons to be discussed further below, quite preliminary. This paper should be read with emphasis on the methodology used, rather than on the numerical values of the results obtained.

MATERIAL AND METHODS

Raw data

The data used for all analyses presented here originally consisted of monthly length-frequency data collected from March 1961 to December 1979 by staff of the Instituto del Mar del Perú (IMARPE) in the ports of Chicama, Chimbote, Samanco and Casma (of these Chimbote accounts for more than 80% of anchoveta landings in the Northern Region). The data analyzed here thus pertain to the northern stock of anchoveta (see IMARPE, 1970 for comments on the status of anchoveta stocks off the Peruvian-Chilean coast).

The sampling procedures for length-frequency samples generally followed those given in Saetersdal and Valdivia (1964), who presented data suggesting that for the stretch of coastline ranging from the Northern to the Central Regions, within port variability of the length-frequency samples was less than variability due to different sampling periods. Monthly samples representative of the northern stock as a whole were obtained by pooling daily samples representing more than 30% of the landings, and most of the fishing areas covered by the fleet. Generally, one single sample was taken from each vessel sampled; the sample consisted of the contents of a two-liter container, of which all anchoveta were measured and weighed. The monthly samples representative of the monthly catches were then raised to the catch.

---

* The first version of ELEFAN III was written by J.G. Pope at Lowestoft, England.

During periods when the commercial fishery was closed, length-frequency data were obtained from 1972 on by sampling during "EUREKA Surveys", and other scientific surveys and cruises. Here, the samples (taken after each haul) were raised to the total catch made during the survey or cruise (see IMARPE, 1972, 1974 for brief accounts of the EUREKA and other surveys and cruises).

The data used all refer to total length, and are grouped in 0.5 cm classes. For the analysis of growth, the data were regrouped into 1 cm classes to obtain a number of length classes of about 20 or less, which is optimum for analysis with ELEFAN I (Pauly et al., 1980).

The full data set used here extended to the period before 1961 and beyond 1979 will be published later, along with an analysis more detailed than that presented here.

Growth

The analysis of length-frequency and catch-at-length data using ELEFAN I is based on the following assumptions (adapted from Pauly and David, 1981):

- the samples used represent the population investigated,
- the seasonally oscillating version of the von Bertalanffy Growth Function (VBGF) describes the average growth of the fish,
- all fish in the samples have the same length at the same age and therefore differences in length can be attributed to differences in age.

Another assumption in Pauly and David (1981), namely "that the growth patterns are the same from year to year" need not apply here as the estimation of growth parameters was performed separately for each year. The last of the three assumptions above certainly does not apply as anchoveta of different sizes can very well be expected to have the same age. The anchoveta, however, is not a long-lived fish, and, as will be shown below, the bulk of a cohort goes through the exploited phase within less than two years, with the result that fish hatched during say, a given month remain identifiable as a group throughout most of their exploited life span (see Saetersdal and Valdivia, 1964 and Fig. 1).

Put briefly, the ELEFAN I program does the following (adapted from Pauly and Ingles, 1981):

- restructures the length-frequency samples that have been entered such that "peaks" are attributed "positive points", and the "troughs" separating peaks "negative points",
- calculates from the positive points of the peaks of all samples entered a sum named "available sum of peaks" (ASP, analogous to the total variance of parametric methods),
- traces a series of growth curves starting from the bases of the peaks, and projects these curves backward and forward in time such as to hit the other samples in the data set and recording all "points" (positive and negative) "hit" by a curve,
- identifies the curve and hence, the growth parameters - which, by passing through most peaks and avoiding most troughs, best "explains" the peaks in the sample set. This curve will have scored the highest number of points, whose sum is called on the "explained sum of peaks" (ESP, analogous to the explained variance of parametric methods).

Given the validity of the assumptions presented above, ELEFAN I can be used to obtain growth parameters that are completely objective, i.e., in which no assumptions as to the age composition of the catch have been incorporated prior to analysis (Pauly and David, 1981).

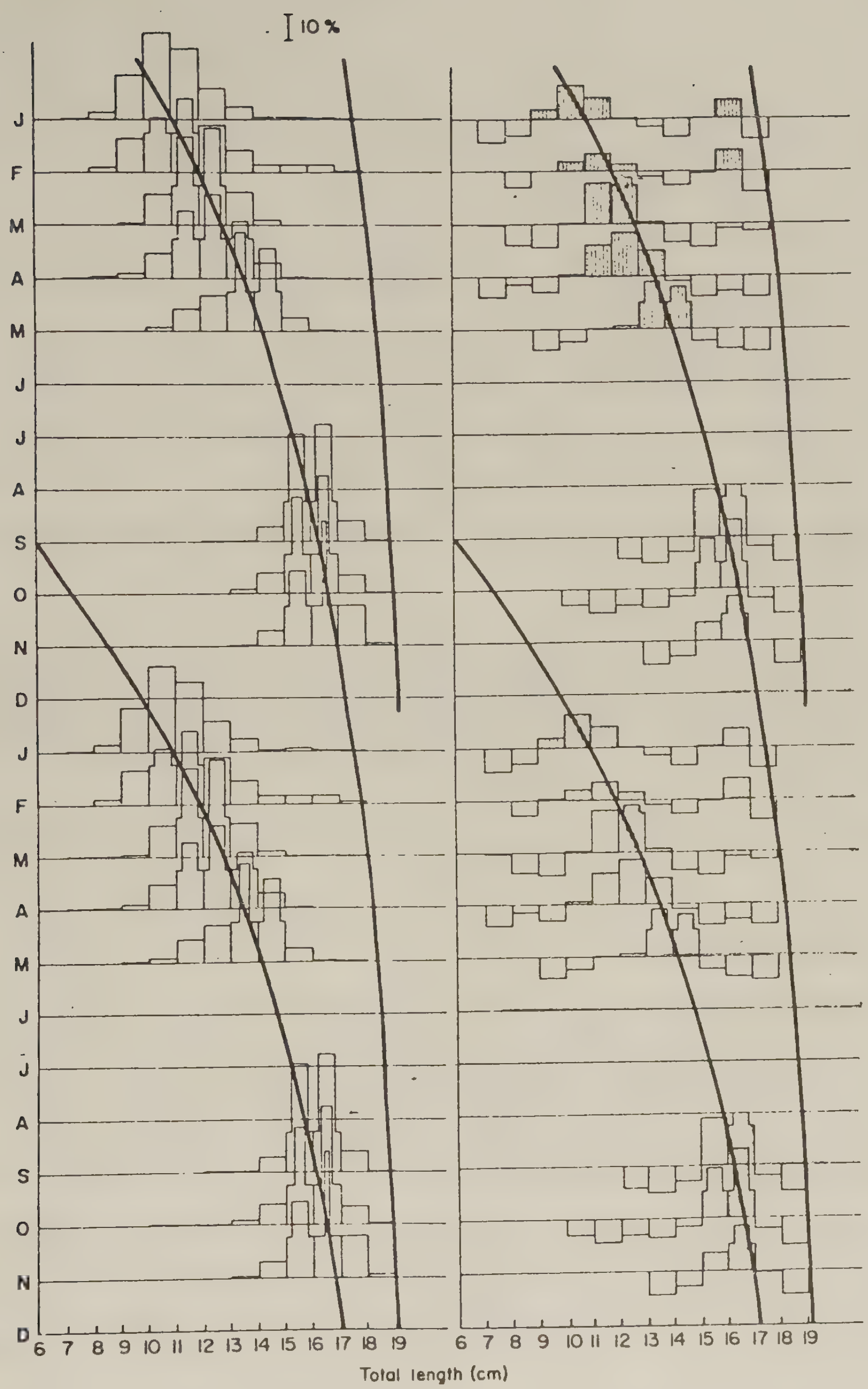


Fig. 1. (Left) Catch-at-lenth data for anchoveta, fitted with a growth curve using ELEFAN I; note "doubling up" of 1970 data to allow for a longer growth curve to be drawn.

(Right) Restructured length-frequency data as used internally by ELEFAN I; note that, through the restructuring process, peaks have become positive "points" (shaded bars) while the troughs separating peaks have become negative "points" (open bars).

The seasonally oscillating version of the VBGF used here has the form

$$L_t = L_\infty (1-\exp (-[[K(t-t_o)] + [\frac{KC}{2\pi} \sin 2\pi \ (t-t_s)]]) \qquad \ldots 1$$

where:

- L_t is the length at age t,
- L_∞ the asymptotic length,
- K a growth constant,
- t_o the "age" at which length is zero if the fish always grew according to the equation,
- C is a dimensionless constant expressing the intensity of the growth oscillations,

and t_s is the time (with respect to t=0) at the beginning of a sinusoidal growth oscillation of period one year (Pauly and Gaschütz, 1979; Gaschütz *et al*., 1980).

In ELEFAN I, the estimation of t_s is replaced by the estimation of a Winter Point (WP), defined as

$$t_s + 0.5 = WP \qquad \ldots 2$$

which expresses (as a fraction of the year) the time during which growth is slowest. It should be mentioned here that ELEFAN I, being based on length-frequency data (rather than length-at-age data) does not allow for the estimation of t_o, hence of *absolute* ages; all "ages" used internally by the program are relative ages, expressed in *relation* to an arbitrary birthdate (the 1st of January).

ELEFAN I was applied to the available data for the years 1969 to 1979, yielding 19 independent estimates of growth parameters.

Virtual Population Analysis

The ELEFAN III program, in its latest version (Pope, *et al*., MS) consists of 4 main routines:

- a routine to convert length-frequency data into catch-at-length data (not used here, as IMARPE data had already been converted),
- a routine to run a conventional age-structured VPA (here termed VPA I), as discussed, e.g., in Pope (1972),
- a routine to run a VPA-version of Jones' (1979, 1981) length-cohort analysis (here termed VPA II, see below), and
- a routine to run an age-structured VPA on catch-at-length data arranged such that they produce the functional equivalents of cohorts (here termed VPA III, see below).

VPA I is based on the equation

$$\frac{N_{i+1}}{C_i} = \frac{Z_i \cdot \exp - Z_i}{F_i \ (1-\exp-Z_i)} \qquad \ldots 3$$

where N_i is the population (in number) at the beginning of time period i, while C_i and F_i are the catch and the fishing mortality during that same time period i. Usually equation (3) is solved (iteratively) backwards, starting from a "terminal population" (N_t) estimated from

$$N_t = \frac{C_t \cdot Z_t}{F_t\ (1\text{-exp-}Z_t)} \qquad \ldots\ 4$$

where F_t is the (assumed) terminal fishing mortality and C_t the terminal catch, while M is the natural mortality which is generally assumed constant throughout (Pope, 1972).

Generalizing equation (3) to any time interval (Δt) gives

$$\frac{N_i + \Delta t}{C_i} = \frac{Z_i \cdot \exp\ (Z_i \cdot \Delta t)}{F_i\ (1\text{-exp-}Z_i \cdot \Delta t)} \qquad \ldots\ 5$$

This equation is a functional equivalent of Jones (1979, 1981) equation for length cohort analysis and can be used to run a VPA on catch-at-length data starting from

$$N_t = C_t \cdot Z_t/F_t \qquad \ldots\ 6$$

and estimating Δt from

$$\Delta t = \frac{1}{K} \cdot \log_e \left\{ \frac{L\infty - L_1}{L\infty - L_2} \right\} \qquad \ldots\ 7$$

i.e., by calculating using the VBGF, the time needed to grow from the lower (L_1) to the upper (L_2) limit of a length class (see Jones, 1981). Equation (5) is used here, instead of the original length-cohort analysis proposed by Jones (1979, 1981) because as shown by Pauly (in press) the VPA version of Jones' method produces results which are insensitive to the width of the length classes into which the catch data are grouped; Pope et al. (MS) and Pauly (in press) give more details on this method.

It must be mentioned, however, that the method does not provide estimates of standing stock and fishing mortality pertaining to a given cohort (as does VPA I); rather the method provides estimates of the population of fish and the fishing mortalities that must have existed for the recorded catches to have been generated (Jones 1981). The method is therefore at its best when catch data from longer time periods are grouped such as to simulate equilibrium conditions.

For this paper, we have grouped the available monthly catch data into years, and thus report estimates of annual recruitment, standing stock and fishing mortality.

VPA III is a version of VPA I performed on "cohorts" obtained by superimposing growth curves, drawn at monthly intervals, onto a set of catch-at-length data, the catch pertaining to each "cohort" and month being simply that part (obtained by addition and interpolation) of a monthly catch contained between two growth curves (see Fig. 2).

For such cohorts to consist of fish recruited at the same time, the growth curves used for "slicing up" a cohort must be obviously as close to the true growth curve of that cohort as possible, which among other things makes it imperative that a seasonally oscillating curve be used since, as shown in Pauly and Ingles (1981) and Pauly (1982), virtually all fish species display seasonally oscillating growth.

In reality, not all fish of a given cohort have the same growth parameters, and it can be expected that some fish will "leave their cohort" because they grow either faster or slower than predicted by the mean growth curve of their cohort. Such differences in growth rate should here have the effect of somewhat smoothing month to month variations in the estimates of fishing mortality and derived parameters.

The VPA III routines of ELEFAN III were applied to the available catch-at-length data using the growth parameters given in Table 1. The small year-to-year differences in the values of the growth parameters caused a slight overlap of some "cohorts" (i.e., some of the catch data were used twice), and small gaps (i.e., some of the catch data were not included in any cohort.) This source of error could have been avoided by using the same growth parameters throughout. This, however, would have caused misidentification of some cohorts.

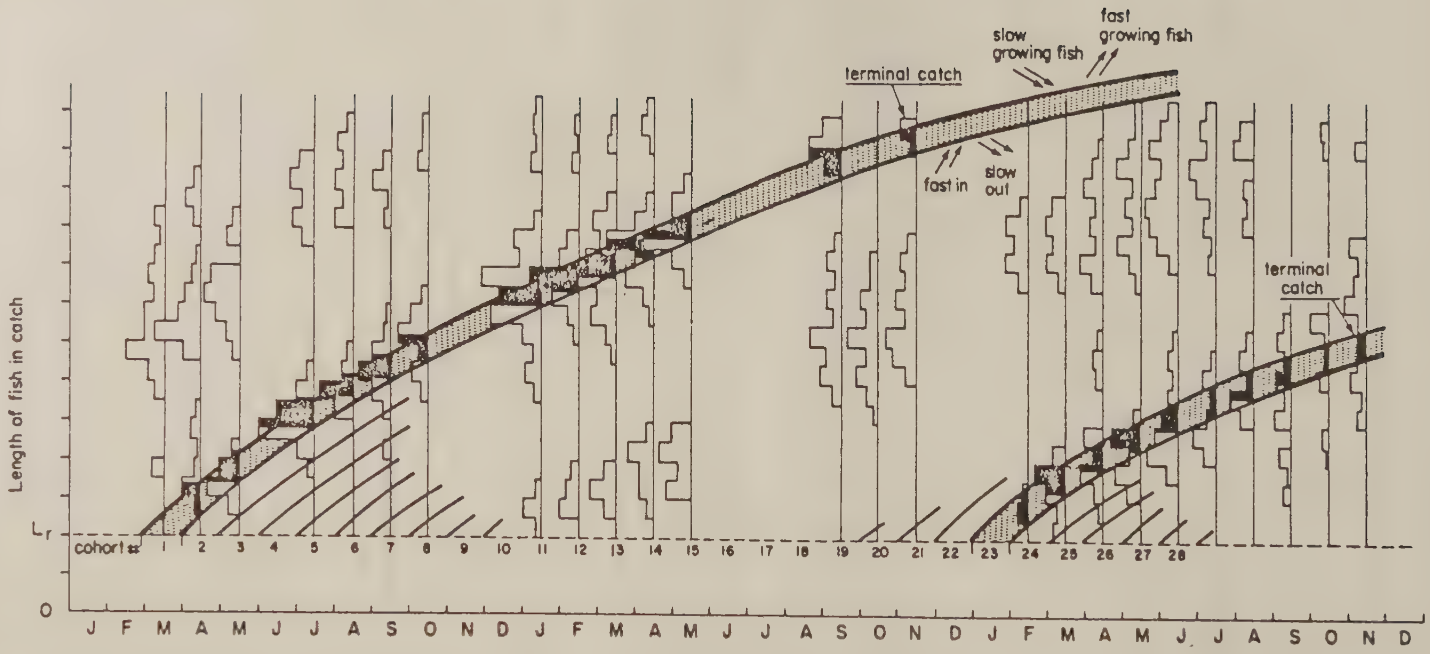

fast
growing fish
slow
growing fish
terminal catch
fast in
slow
out
terminal
catch
Length of fish in catch
L_r
0
cohort #
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D

Fig. 2. Schematic representation (not to scale) of VPA III as implemented in ELEFAN III. Two "cohorts" (#1 and 23) are shown; they are defined by the growth parameters of the growth curves on their upper and lower boundaries, and by that part of the catch (black histograms) comprised between these boundaries. The terminal catches are shown. Note (partial) compensation of fish leaving a "cohort" (due to slower or faster growth) by fish from neighboring cohorts. Length at recruitment (L_r) is defined by smallest fish in catch.

Table 1: Growth parameters of Peruvian anchoveta (*Engraulis ringens*, northern stock) as estimated by means of the ELEFAN I computer program.

Year	L_∞ (cm)	K (per year)	WP[a]	C[a]	ESP/ASP
1961	19.65	1.26	(0.6)	(0.2)	0.572
1962	20.75	1.16	0.8	0.35	0.513
1963	18.95	1.39	0.8	0.3	0.439
1964	20.70	1.22	0.6	0.23	0.588
1965	20.75	1.21	0.6	0.4	0.503
1966	20.75	1.30	0.65	(0.3)	0.475
1967	20.05	1.36	0.9	0.3	0.655
1968	20.95	1.205	0.96	0.32	0.655
1969	20.95	1.19	0.6	0.23	0.570
1970	19.55	1.39	0.8	0.3	0.832
1971	20.75	1.30	(0.75)	(0.3)	0.532
1972	20.70	1.27	0.7	0.3	0.421
1973	20.95	1.20	0.5	0.3	0.598
1974	21.85	1.20	0.5	0.2	0.504
1975	21.25	1.16	0.5	0.2	0.581
1976	21.25	1.31	0.85	0.3	0.420
1977	21.05	1.31	0.8	0.3	0.519
1978	20.75	1.2	0.6	0.4	0.787
1979	20.75	1.215	0.82	(0.3)	0.458
$\bar{x}$	20.65	1.26	0.70	0.30	-
s.d.	0.681	0.073	0.147	0.061	-
C.V. (in %)	3	6	21	20	-
95% confidence interval	±0.31	±0.033	±0.070	±0.031	-

[a] values in brackets are set values; they were not used for the computation of means or confidence intervals.

Preliminary computations suggest that the errors in the recruitment and standing stock estimates are of about ± 15%, which is quite acceptable given the uncertainties involved in such important parameters as natural mortality and terminal fishing mortality (see below).

A value of M=1.2 (annual basis) was used throughout, for both VPA II and VPA III. This value has been used previously by several authors (e.g. Ricker, 1975, p. 197), and was obtained as the intercept of a plot of Z (obtained from catch curves) on effort (T. Burd, pers. comm. in Schaefer, 1967).

A terminal fishing mortality $F_t=1.2$, corresponding with M=1.2 to an exploitation rate (E=F/(F+M)) of 0.5 was used to estimate terminal populations for both VPA II (using Equation 6) and VPA III (using Equation 4). Since E=0.5, as will be shown below, was reached in the mid-60's, the terminal populations have been underestimated in the earlier years, and overestimated in the later years.

Size at recruitment was defined as 4 cm, i.e., slightly less than the 5 cm value used by other authors. It must be considered that, in any case, true catches of "peladilla" (small anchoveta) are underestimated because the fish often disintegrate before processing.

The mean size at first maturity (i.e., the size distinguishing adults from juveniles) used here was a constant set at 11 cm. This is slightly lower than the 12 cm figure suggested by other authors (Saetersdal and Valdivia, 1964; Murphy, 1972). This size was chosen to account for cases (during El Niño events) where fish reach maturity at much reduced sizes (Tsukayama and Alvarez, 1981).

Biomasses were estimated by multiplication of computed population size (by length) with fish weights, the fish weights being estimated from

$$W = a \cdot L^b \qquad \ldots 8$$

Values of a=0.0065 and b=3 were used throughout, with length expressed in centimeters and W in grams. At this stage of our analysis, we made no efforts to account for within and between years variations of the length/weight relationships, although we are aware that such variations occur (IMARPE, 1976, 1977a, 1977b, 1980, 1981, 1982), and may cause under- or over-estimates of standing stock.

All computer-based analyses were performed on a Radio Shack TRS 80 Model III microcomputer.

RESULTS

Growth

Table 1 gives 19 estimates of the values of the growth parameters L , k, C and WP for the period 1961 to 1979. As might be seen, there was no trend over time in any of the parameters and it can therefore be stated that the parameters describing the growth *in length* of the northern stock of the Peruvian anchoveta have been more or less constant from the period 1961 to 1979, despite large changes in biomass (this does not preclude changes in the growth *in weight*, see above).

The mean value of C=0.30 suggests that the growth of anchoveta oscillates seasonally in sinusoidal fashion, and that it is, during the warmest summer month, 30% higher than it would be if no oscillations occurred. Conversely, the growth of anchoveta is reduced in winter, down to a 30% reduction during the coldest month; "winter" as perceived by the anchoveta occurs at WP=0.70 ± 0.07, corresponding to the 12th of September (± 26 days). The temperature data in Zuta and Urquizo (1972) show that sea surface temperatures off Peru oscillate in sinusoidal fashion, with most common values for minima and maxima occurring in September and March, respectively.

The range of the oscillation of mean monthly temperature, moreover, is 3 to 6°C; these values correspond well to the mean value of C (which expresses the intensity of the growth oscillations) reported here (Fig. 3).

Two important points must be borne in mind when considering these results:

- the values of C and WP were extracted from length-frequency data, yet match very well the values that would have been predicted on the basis of the temperature regime off Peru alone and
- the oscillations reported here are generally too faint to be perceived, let alone quantified using standard methods (i.e., eye-fitting) for the analysis of length-frequency data.

VPA II

Table 2 summarizes the results obtained using VPA II (Table 3 gives an example, pertaining to 1968, of the output obtained from ELEFAN III).

VPA III

The estimates of recruitment (R), adult stock (S), values of $\log_e$ (R/S), the catches, total biomass and estimates of fishing mortality are presented as monthly values for the period 1961 to 1979 in Figs. 4 to 9.

The values of $\log_e$ (R/S) in Fig. 6 are in fact values of $\log_e (R_i/S_{i-1})$, i.e., the recruitment of a given month was plotted against the adult biomass of the preceding month. Fig. 14 in Saetersdal and Valdivia (1964) suggests that 4 cm fishes are generally between 1 and 2 months old.

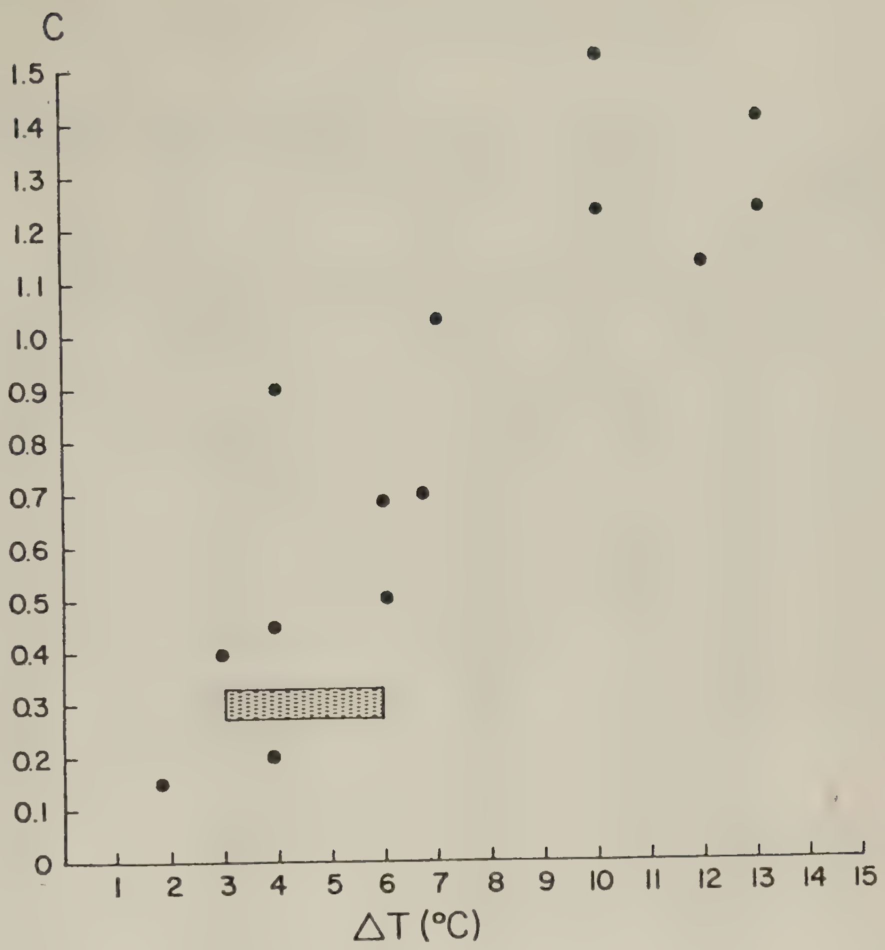


Fig. 3.
Values of C (expressing the intensity of seasonal growth oscillations) plotted against Δ T (expressing the difference between warmest and coldest mean monthly water temperature) in a number of tropical and temperate fishes. The shaded area, referring to the anchoveta, is based on the C values in Table 1 and range of Δ T values in Zuta and Urquizo (1972). Note that the seasonal oscillations in the growth of anchoveta conform to the general pattern established for other fishes by Pauly and Ingles (1981).

Table 2: Results of VPA II for the years 1961[a] to 1979.

Year	Recruitment[b]	Catch[c]	$\bar{E}^{d}$	$\bar{F}^{e}$	$\bar{B}^{c,\ f}$
1960	212	-	-	-	-
1961	317	1314	0.39	0.77	1713
1962	295	2194	0.39	0.75	2908
1963	509	1908	0.40	0.81	2365
1964	353	3429	0.47	1.07	3197
1965	434	2290	0.46	1.01	2258
1966	479	2903	0.52	1.33	2177
1967	579	3837	0.33	0.58	6581
1968	547	4351	0.36	0.68	6418
1969	626	3293	0.51	1.26	2616
1970	483	4028	0.46	1.03	3909
1971	127	3289	0.49	1.14	2887
1972	359	910	0.38	0.72	1264
1973	159	321	0.48	1.11	289
1974	114	744	0.35	0.64	1157
1975	132	852	0.34	0.61	1391
1976	22.5	566	0.61	1.88	302
1977	8.72	135	0.51	1.24	109
1978	61.6	425	0.51	1.26	336
1979	-	321	0.46	1.00	320

[a] The January 1962 and February 1962 catches were added to the 1961 catch (March to December) to obtain 1961 figures comparable to those of the other years.

[b] The catch of a given year was used to infer recruitment the preceding year; this is an approximation (see text); recruitment refers to number of 4 cm fish (x 10^9).

[c] In tonnes (x 10^3)

[d] Obtained from E=number of fish caught/number of fish dying of all causes; latter number is approximated by the recruitment itself, since all fish recruited finally die.

[e] Obtained as $F=(M/(1-E))-M$.

[f] Obtained from $\bar{B}$=catch in weight/mean fishing mortality.

Table 3: Results of VPA II for the year 1968
(see Table 2).

```
 <<<<<   VPA 2 RESULTS FOR ENGRAULIS RINGENS 1968   >>>>>

  LENGTH            CATCHES           POPULATION        FISH. MORTALITY

  19 - 19.5         3                 6                 1.2
  18.5 - 19         17                25.768            7.37504
  18 - 18.5         106               143.361           10.9724
  17.5 - 18         1056              1274.2            16.9331
  17 - 17.5         4349              6008.53           13.5436
  16.5 - 17         11183             18433             10.8091
  16 - 16.5         19061             40308.8           8.12607
  15.5 - 16         36190             81861.2           8.09872
  15 - 15.5         36383             126845            5.07618
  14.5 - 15         34147             172461            3.57291
  14 - 14.5         12637             198366            1.14295
  13.5 - 14         5840              218118            .503711
  13 - 13.5         2809              235119            .237521
  12.5 - 13         4008              253521            .334135
  12 - 12.5         3614              271744            .29685
  11.5 - 12         4647              291220            .376049
  11 - 11.5         4272              310547            .340511
  10.5 - 11         3933              329733            .309429
  10 - 10.5         2788              347927            .217158
  9.5 - 10          3135              366598            .24216
  9 - 9.5           2372              384620            .18188
  8.5 - 9           2204              402564            .168023
  8 - 8.5           1381              419754            .104829
  7.5 - 8           1007              436612            .0762341
  7 - 7.5           492               452980            .0371876
  6.5 - 7           186               469052            .0140503
  6 - 6.5           47                484987            3.54992E-03
  5.5 - 6           5                 500878            3.77701E-04
  5 - 5.5           17                516780            1.28429E-03
  4.5 - 5           8                 532671            6.04442E-04
  4 - 4.5           4                 548556            3.02256E-04

 TOTAL CATCH = 197901   MEAN E = .360767   MEAN F = .677251
```

Fig. 4.

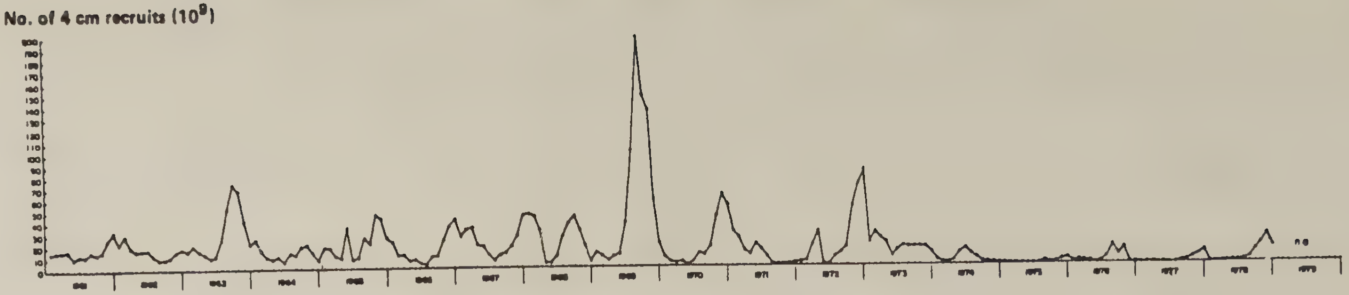


Fig. 5.

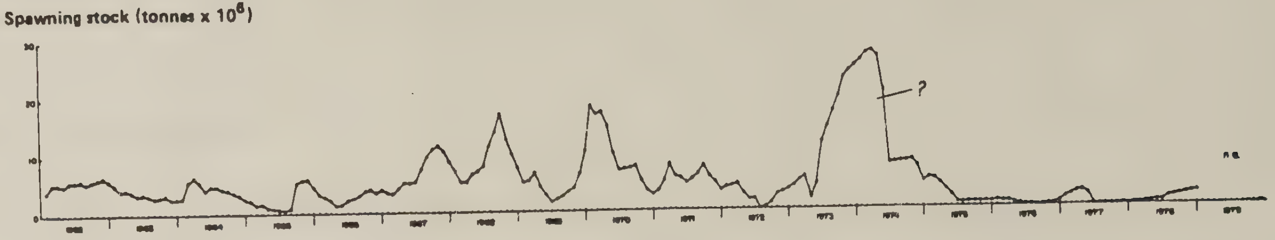


Fig. 6.

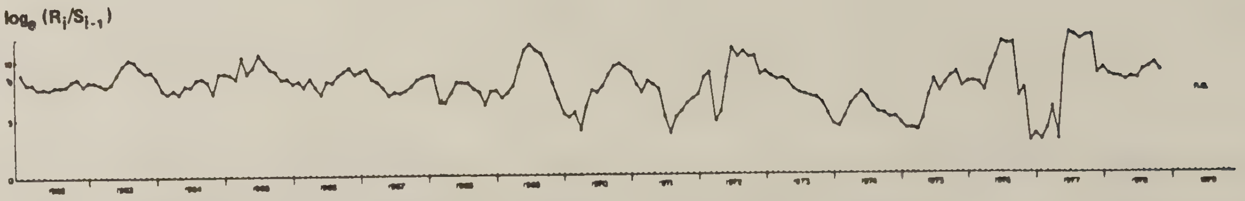


Fig. 4. Monthly recruitment to the northern stock of Peruvian anchoveta, 1961 to 1978. Overall, this time-series matches closely the sequence of events given by previous authors, particularly Cushing (1981).

Fig. 5. Monthly estimates of adult biomass (defined as fish > 11 cm, see text). Overall, this series matches most of the estimates in previous works, notably IMARPE, 1970, 1972, 1973 and 1974 and Cushing, 1981. Differences may be explained by large differences in approaches used. The enormous increase in 1973-1974 may be an artifact due to the use of unrealistic values of M (see text).

Fig. 6. Time series of $\log_e (R_i/S_{i-1})$. This index would be a direct expression of egg and larval survival if adult fish spawned every month an amount of eggs proportional to their biomass. As used here, it expresses both "non-spawning" and survival of pre-recruits. Nevertheless, a close association between this index and El Niño events will be noted.

Fig. 7.

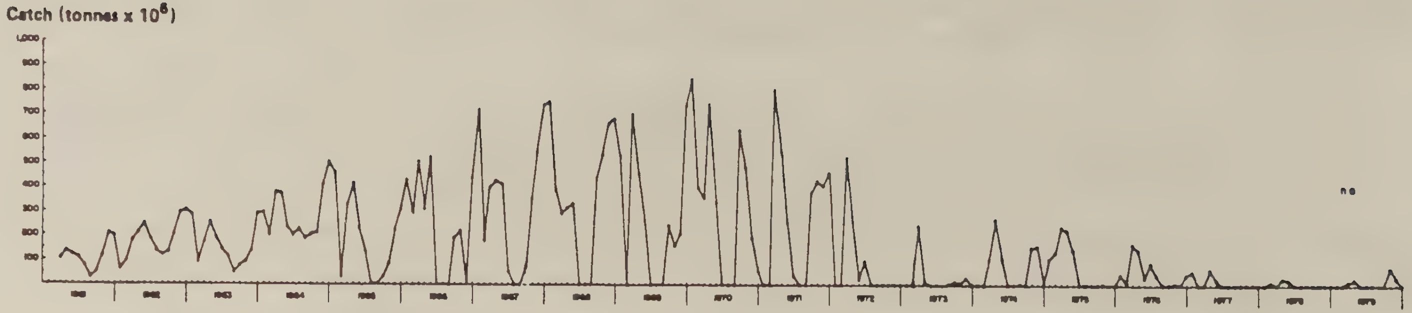


Fig. 8.

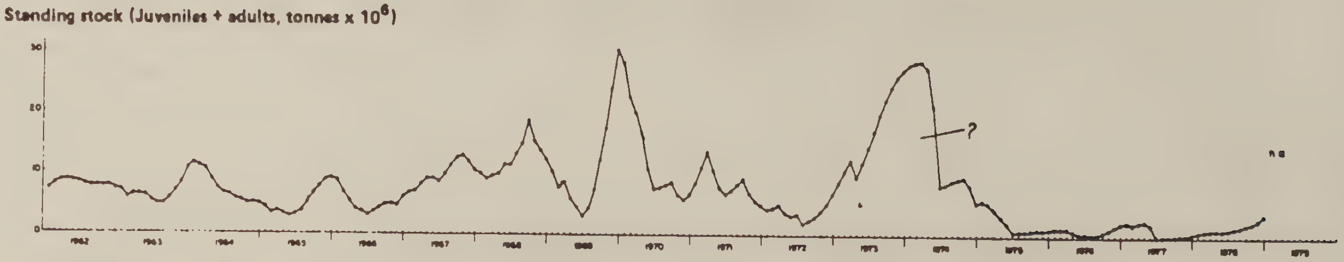


Fig. 9.

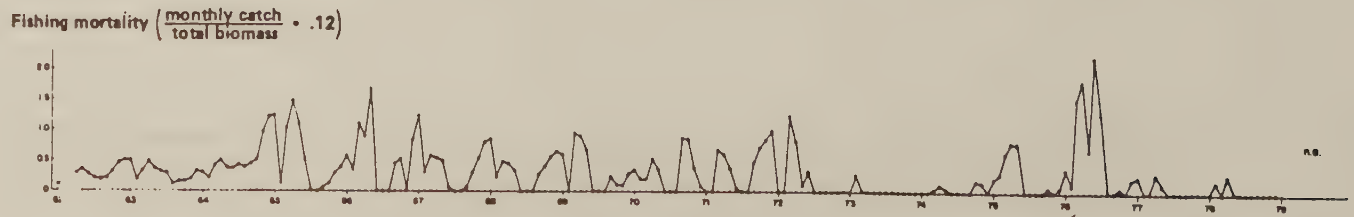


Fig. 7. Monthly catch of anchoveta, northern stock, 1961 to 1979. Zero catches represent periods of closure, not of zero availability of fish.

Fig. 8. Time series of total anchoveta biomass (adults and juveniles, but excluding fish $<$ 4 cm), northern stock. Major sequence of events as expressed here match earlier accounts, except for enormous increases in 1973-1974 which may be an artifact due to the use of unrealistic values of M (see text).

Fig. 9. Estimated values of fishing mortality (F) obtained by dividing catches in Fig. 7 by biomasses in Fig. 8. Obviously, errors in the biomass estimates will be reflected in the values of F which, therefore, should be considered as tentative.

DISCUSSION

The following parameter values are now available on the growth of *Engraulis ringens*:

L (cm)	K (per year)	Source
15	1.7	Saetersdal and Valdivia (1964)
16.8	1.4	Chirinos de Vildoso and Chumán (MS)
18.5	1.1	Tsukayama and Zuzunaga (MS)
19.0	1.11	Simpson and Buzeta (1967)
20.65	1.26	this study (Table 1)

Of the parameter values obtained previously, those of Tsukayama and Zuzunaga (MS) and those of Simpson and Buzeta (1967) appear most reasonable, especially in view of the fact that old *E. ringens* may reach a length of 17-18 cm. We believe the discrepancy between our estimates and the two earlier sets is due to our having considered seasonal growth oscillations; thus what here appears as the acceleration (due to a summer spurt) of an otherwise steady growth presumably has been interpreted as a rapid growth toward a smaller maximum size.

In any case, our results are similar to those of other authors in that they imply that anchoveta, once recruited, may stay about two years in the fishery, notwithstanding the return of a fish tagged up to 5 years previously (Cushing 1981).

The most interesting part of the growth study presented here is, we believe, the demonstration and quantification of growth oscillations which so closely fit the general pattern derived from the study of a number of other fish species (Fig. 3).

This is encouraging because it implies that the anchoveta is not such a special fish after all, and that parameter values (e.g., for use in simulation modelling) detained from stocks similar to the Peruvian anchoveta may be used.

The application of VPA II does not seem to be useful in the case of a short-lived fish such as the anchoveta, where the stock size may fluctuate violently within periods of a few months. Inherent to the VPA II method is, it is recalled, the need to group data over a period of time when conditions are somewhat constant, which was hardly ever the case off Peru. Based on the present experience, it seems now that it would be most appropriate to limit the application of this method to stocks of long-lived animals in which recruitment fluctuations cause only ripples in the size of the accumulated stock.

VPA III, on the other hand, seems eminently suited to study the dynamics of anchoveta as reasonable estimates of recruitment, biomass, fishing mortality and other quantities could be derived with an extremely limited amount of data beyond the catch data themselves. However, the number presented here could all be rendered more accurate by considering the following:

(1) the assumption of constant mortality (M=1.2) used here certainly does not apply, and subsequent applications of VPA III to the anchoveta stock should take this into account, e.g., by expressing natural mortality as a function of the biomass of their major predators (guano birds, certain fishes). This should help bring the standing stock estimates for 1973-1974 (Figs. 5 and 8) down to more realistic values, among other things;

(2) the terminal fishing mortalities used to initiate the VPA's should not be constant either, but rather should reflect the increase in F noted, e.g., in this study;

(3) the conversion of fish numbers to biomass should take into account the changes in condition factor reported for the anchoveta;

(4) the catch data from the "northern stock" should be pooled with at least those from the "central stock" to account for the large exchanges known to occur between these stocks;

(5) the time series should be if possible extended back in time to obtain more data reflective of a situation when between-month variability in stock size was reduced, and forward in time to include more data from that period when the anchoveta was supplanted by other pelagics.

Given these adjustments and improvements, we believe that the method presented here could lead to significant insights into the mechanisms which determine anchoveta recruitment: The large number of stock and recruitment values obtained will allow the testing of a larger number of variables (biotic and abiotic) for their effect on $\log_e$ (R/S), as suggested by IMARPE (1973) and performed (with only 2 variables) by Csirke (1980). However, as noted by Bakun et al. (1982) "there is always an extremely limited number of data points available (one per year). Thus, the number of explanatory variables must be reduced to a minimum".

The VPA III approach presented here overcomes this constraint, as 12 values of stock size and recruitment are generated per year. Thus, we have here 203 data points enough to test a large number of variables for their effect on $\log_e$ (R/S) (including dummy variable(s) for the "spawning season" itself).

We believe that it is the last mentioned aspect of the methodology proposed here which has the greatest potential, because having a large number of relatively independent data points offers the real possibility of identifying and quantifying factors with crucial impact on recruitment. Such factors, once identified, will certainly allow better yield predictions to be made.

ACKNOWLEDGEMENTS

We wish to thank all IMARPE staff, present and past for their contribution to the data used here especially Mrs. Maria Alvarez, Mr. J. Pellōn, A. Haro, M. Flores and to Noel David at ICLARM for faithfully adapting ELEFAN III to our everchanging needs. Also, we wish to thank Dr. W. Arntz (Projecto Peruano-Alemān de Cooperaciōn Pesquera, Callao) for inviting one of us (DP) to Peru, and J.A. Gulland (FAO, Rome) for reading and suggesting improvements to a draft of this paper. Last, but certainly not least, we wish to thank Miss Lourdes "Deng" Palomares (ICLARM) for actually running all these data through the ELEFAN programs.

REFERENCES

Bakun, A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean sciences in relation to living resources. Can.J.Fish.Aquat.Sci. 39(7):1059-1070.

Boerema, L.K., G. Saetersdal, I. Tsukayama, J. Valdivia, and B. Alegre. 1967. Informe sobre los efectos de la pesca en el recurso peruano de anchoveta. Bol.Inst.Mar.Perú. 1(4):133-186.

Chirinos de Vildoso, A. and E. Chumán. Un estudio del crecimiento de la anchoveta (Engraulis ringens, J.) basado en la lectura de otolitos. (MS).

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp.P.-v.Réun.Cons.Int.Explor.Mer. 177:307-313.

Cushing, D.H. 1981. The effect of El Niño on the Peruvian anchoveta stock. In Coastal upwelling (F.A. Richards, ed.). Coastal and Estuarine Sciences 1. American Geophysical Union, Washington, D.C.

Gaschütz, G., D. Pauly and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. I.C.E.S. C.M. 1980/D:6 Statistics Committee. 14 p.

Glantz, M.H. and J.D. Thompson (eds). 1980. Resources management and environmental uncertainty: lessons from coastal upwelling fisheries. Wiley Interscience, New York.

Gulland, J.A. 1968. Informe sobre la dinamica de la población de anchoveta peruana. Bol.Inst.Mar Perú. 1(6):305-346.

IMARPE. 1970. Report of the panel of experts on population dynamics of Peruvian anchoveta. Bol.Inst.Mar Perú. 2(6):324-372.

____________. 1972. Report of the second session of the panel of experts on the population dynamics of Peruvian anchovy. Bol.Inst.Mar Perú. 2(7):373-458.

____________. 1973. Report of the third session of the panel of experts on the population dynamics of Peruvian anchovy. Bol.Inst.Mar Perú. 2(9):525-599.

____________. 1974. Report of the fourth session of the panel of experts on stock assessment of Peruvian anchoveta. Bol.Inst.Mar Perú. 2(10):605-719.

____________. 1976. La situación de la población de anchoveta y su pesquería hasta mediados de abril de 1976. Informe al Despacho Ministerial.

____________. 1977a. El recurso anchoveta, el medio ambiente, la regulación de su pesquería desde 1960 a 1977 y sus perspectivas. Informe al Despacho Ministerial.

____________. 1977b. Situación de los stocks de anchoveta y otros recursos pelágicos durante el segundo semestre de 1977. Informe al Despacho Ministerial.

____________. 1980. Informe de evaluación de los recursos pesqueros anchoveta, sardina, jurel y caballa a julio 1980. Inf.Inst.Mar Perú. No.78.

____________. 1981. Informe de seguimiento de las pesquerias de recursos pelágicos de enero a julio 1981. Addenda: Pescas agosto-setiembre 1981. Informe al Despacho Ministerial.

____________. 1982. Informe de seguimiento de las pesquerías de recursos pelágicos durante el periodo enero-setiembre 1982. Informe al Despacho Ministerial.

Jones, R. 1979. An analysis of Nephrops stocks using length composition data. Rapp.P.v.Réun.Cons. Int.Explor.Mer. 175:259-269.

____________. 1981. The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis). FAO Fish.Circ. (734):55 p.

Murphy, G.I. 1972. Fisheries in upwelling regions, with special reference to Peruvian waters. Geoforum. 11:63-71.

Pauly, D. 1982. Studying single-species dynamics in a multispecies context. In Theory and management of tropical fisheries (D. Pauly and G.I. Murphy, eds). ICLARM Conference Proceedings 9. International Center for Living Aquatic Resources Management, Manila.

____________. (In press). Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews.

Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforschung. 28(4):205-211.

Pauly, D. and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculator. I.C.E.S. C.M. 1979/G:24 Demersal Fisheries Committee. 26 p.

Pauly, D. and J. Ingles. 1981. Aspects of the growth and natural mortality of exploited coral reef fishes. In The reef and man. Proceedings of the fourth international coral reef symposium (E.D. Gomez, C.E. Birkeland, R.W. Buddemeier, R.E. Johannes, J.A. Marsh, Jr. and R.T. Tsuda, eds). Vol.1. Marine Sciences Center, University of the Philippines, Diliman, Quezon City.

Pauly, D., N. David and J. Ingles. 1980. ELEFAN 1: user's instruction and program listings. International Center for Living Aquatic Resources Management, Manila. (Mimeo) pag.var.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int.Comm.Northwest Atl.Fish.Res.Bull. 9:65-74.

Pope, J.G., D. Pauly and N. David. ELEFAN III, a BASIC program for the detailed analysis of catch-at-length data using Virtual Population Analysis. International Center for Living Aquatic Resources Management, Manila. (MS).

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull.Fish.Res.Board Can. 191:382 p.

Saetersdal, G. and J.E. Valdivia. 1964. Un estudio del crecimiento, tamaño y reclutamiento de la anchoveta (Engraulis ringens, J.). Bol.Inst.Invest.Rec.Mar. 1(4):85-136.

Schaefer, M.B. 1967. Dynamics of the fishery for the anchoveta Engraulis ringens off Peru. Bol.Inst.Mar Perú. 1(5).

Simpson, J.G. and R. Buzeta. 1967. El crecimiento y la edad de la anchoveta (Engraulis ringens, Jenyns) en Chile, basado en estudios de frequencia de longitud. Inst.Fom.Pesq.Bol.Cient. 3:53 p.

Tsukayama, I. and M.A. Alvarez. 1981. Fluctuaciones en el stock de anchovetas desovantes durante los ciclos reproductivos de primavera 1964-1978. pp. 233-240. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes (G.D. Sharp, ed.). IOC Workshop Report No.28. IOC/UNESCO, Paris.

Tsukayama, I. and J. Zuzunaga. Crecimiento de anchoveta en base a distribución por tamaños. (MS).

Zuta, S. and W. Urquizo. 1972. Temperatura promedio de la superficie del mar frente a la costa Peruana periodo 1928-1969. Bol.Inst.Mar Perú. 2(8):459-520

BODY LENGTH VARIABILITY IN FISH SCHOOLS AND COHORTS; APPLICATION TO FISHERIES BIOLOGY IN TROPICAL WATERS

(Summary only)

by

Pierre Fréon

ORSTOM 24
rue Bayard 75008
Paris, France

SUMMARY

In pelagic fish populations, individuals of similar size assemble in schools, which can be defined as a physical grouping of gregarious fish "mutually attracted to each other" (Shaw, 1980). The fishery biologist is more interested, in the dynamics of population studies, by the concept of cohort defined as a set of animals from the same species and issue from a same spawning period, but this concept seems to be ignored by the fish.

Except for size, a cohort or a school is mainly characterised by the mean length of individuals and by the spread around this mean. The relations between these two parameters have been studied in cohorts and schools of tropical small pelagic fish, in order to improve the knowledge of fish aggregation mechanisms and their consequences on fisheries biology.

From a theoretical point of view, if each individual is assumed to grow according to the Von Bertalanffy's equation with fixed parameters but these parameters differ among individuals, it is then to be expected that variability in length at a given age is mainly due to three factors; first: differences in birth dates (to_i), second: differences between growth rates (k_i), and third: differences between maximal length ($L_{\infty i}$) for adults (Fig. 1).

Data from sardine-like fish (mainly *Sardinella aurita*) in the Central-East Atlantic and from menhaden (*Brevoortia tyrannus*) in the Central-West Atlantic have been studied. This analysis, applied to cohorts, shows an early decrease in the standard deviation of length when plotted against mean length, which suggests a stronger influence of variation in to_i and k_i comparatively to $L_{\infty i}$ (Fig. 2). As applied to schools, the standard deviation of length increases constantly with mean length, providing a constant coefficient of variation. For schools of mixed species, the results are the same, suggesting that regroupment is more related to length similarities than to species groups (Fig. 3).

Comparison between figures obtained from cohorts and schools belonging to the same species shows an inadequacy of length spread between these two structures (Fig. 2). In consequence the scheme of small pelagic aggregations can be summarized in the following three stages:

- during the first stage, not observed under natural conditions, it is possible for fish issued from a same cohort and born within few days interval to remain grouped in the same school or in schools with similar length frequency distributions;

- however, the data strongly suggest that a cohort rapidly disperses into schools of narrower length spread, due to the high degree of variability in the cohort, especially for tropical species which present a spawning period spread over a long time and have high growth rates;

- during the third stage, the cohort length variability decreases to such a degree that it is possible to encounter fish from different cohorts in the same school.

In general a school cannot be considered as representative of the cohort length frequency distribution (Fig. 4).

In pelagic fisheries, the school corresponds generally to the catch unit target and the concept of cohort does not have anymore meaning for fishermen than for fish. It is then the fisheries biologist who must estimate the numerical importance of cohorts through complex sampling methods. The usual stratified sampling methods are recommended, but it is often difficult to define homogeneous strata due to species migrations not related to fishing grounds.

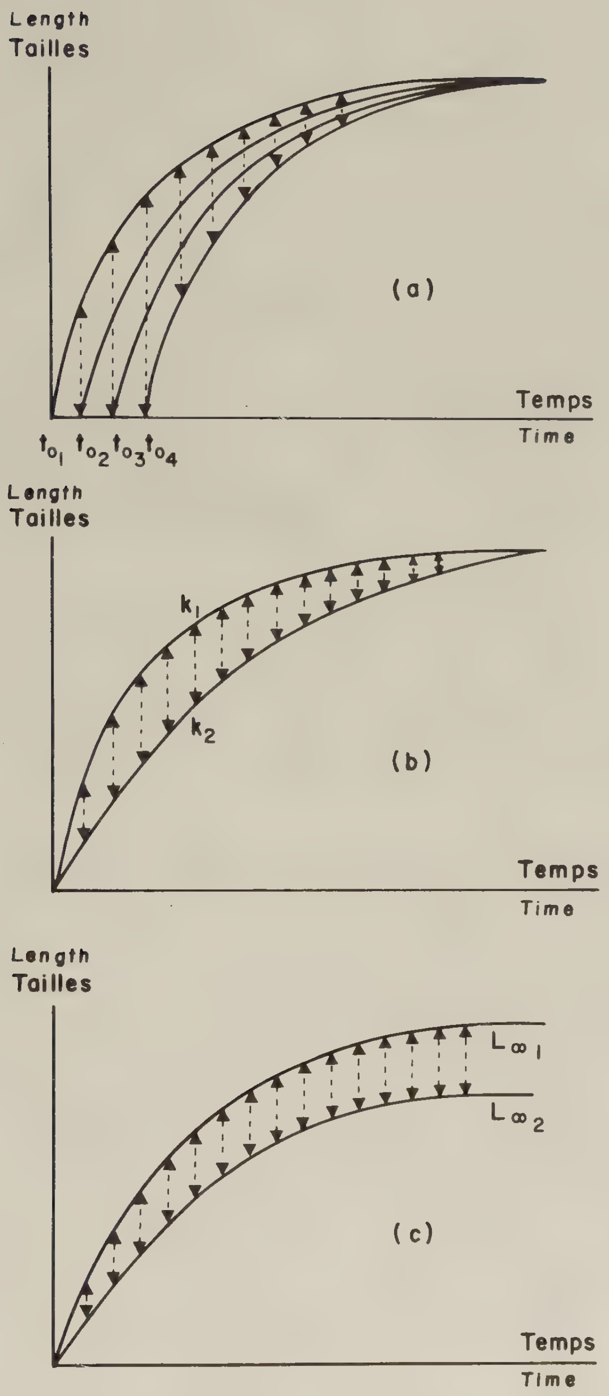

Length
Tailles
(a)
Temps
Time
t_{o_1} t_{o_2} t_{o_3} t_{o_4}
Length
Tailles
k_1
k_2
(b)
Temps
Time
Length
Tailles
L_{∞_1}
L_{∞_2}
(c)
Temps
Time

Fig. 1. Theoretical sources of variability inside a cohort which individuals would present different parameters of Von Bertalanffy's equation.

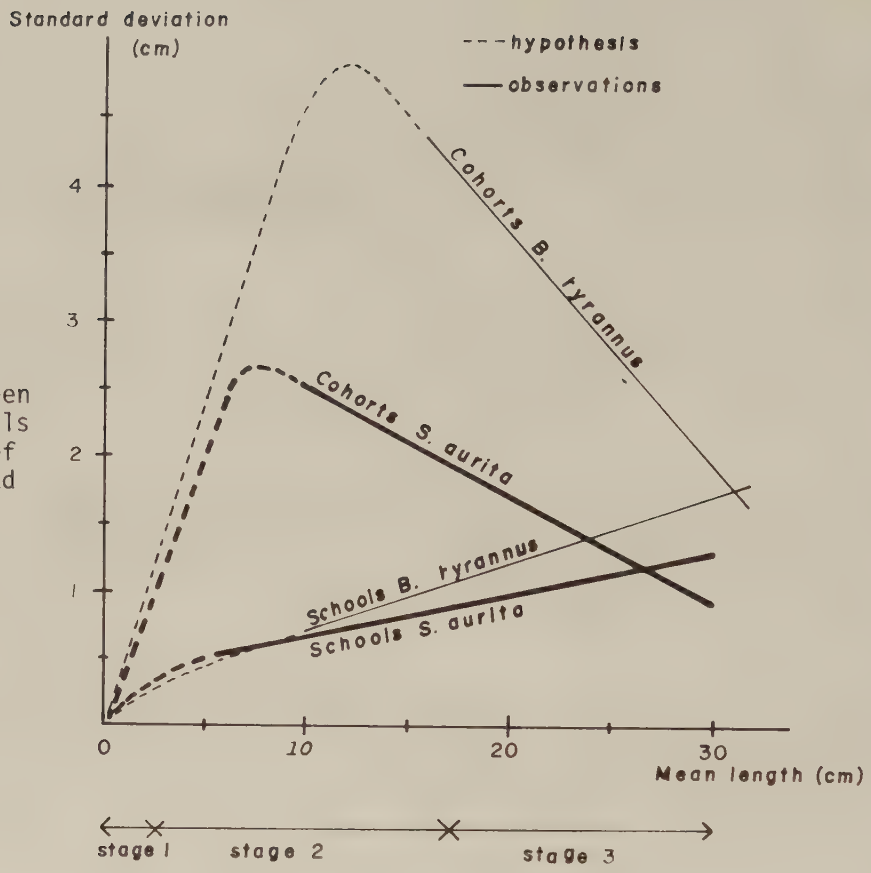


Fig. 2.
Combined scheme showing apparent relations between mean length of individuals and standard deviation of length inside cohorts and schools of *Sardinella aurita* and *Brevoortia tyrannus*.

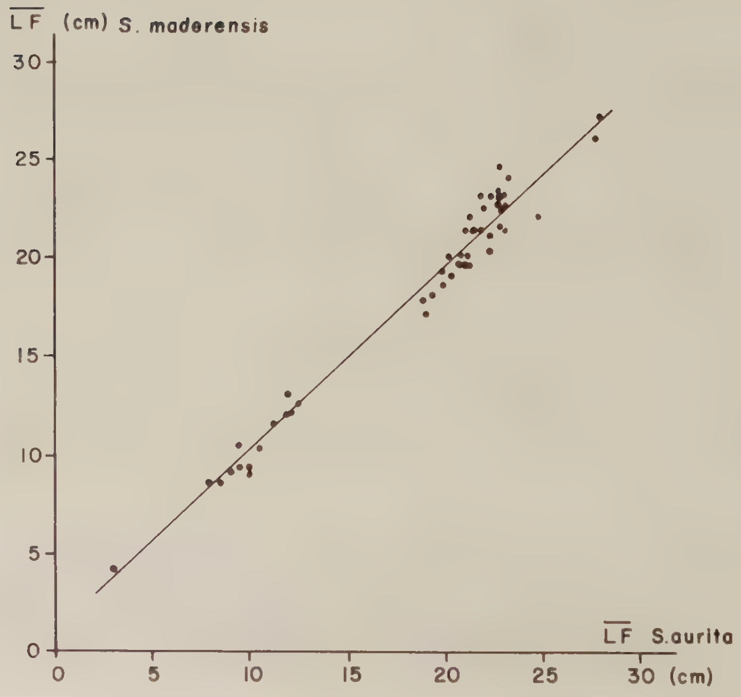


Fig. 3.
Relationship between individual mean length (LF) of *Sardinella aurita* and of *Sardinella maderensis* when encountered in the same school.

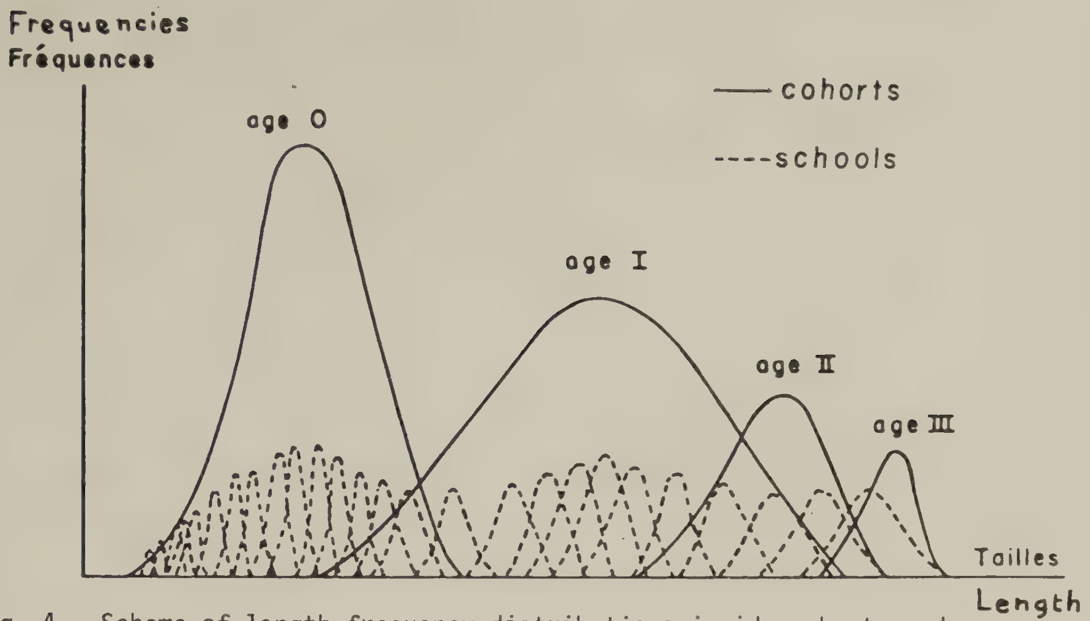


Fig. 4. Scheme of length frequency distributions inside cohorts and schools (to improve scheme understanding, frequency scale is greater for schools than for cohorts).

Fish concentrations where several schools with similar length and age distributions flock together, theoretically constitute ideal strata. However they are often difficult to identify, except in some cases as the sardine fishery in Senegal. Furthermore, homogeneity of concentration is probably not a universal rule valid for all small pelagic species. This homogeneity is needed at the highest level if the double sampling method on length and age is used, because it supposes a similar age distribution inside length classes for different schools within the same concentration.

Contrary to bottom trawls, most of small pelagic fishing gears are not length selective inside the exploited fraction of the population, and under these circumstances the fisheries biologist is indeed happy. Unfortunately, the aggregation mode in coastal pelagic species is such that a school catch, realized with a purse seine for example, can be considered as a catch realized by a very selective trawl-net (mesh-size selectivity and avoidance) on a randomly distributed population, using as many trawl types as there are school types. For this reason, as for demersal species, one must be careful in the choice of sampling methods used to determine age-length keys or growth parameters through hard body part studies. Furthermore, when Petersen's method or derivations are used for indirect growth rate estimations, the hazard is to assign an age class to a modal length class corresponding to nothing more than a school or a concentration which has been over-sampled. Using this method will be much more dangerous if applied to non-regrouped samples, which is commonly done for studying young fish growth. Modal progression with respect to time obtained by such methods can be non-related with growth.

Because of high individual growth rate in tropical coastal pelagic fish, the usual computation of Von Bertalanffy's growth equation parameters for the whole population introduces an under estimate of K, especially if data on growth increment are considered, and not age composition.

In some cases, the biomass percentage of a specific species when encountered mixed with other species in schools is more than 60%. It is then impossible to think in any form of mono-specific model of exploitation.

All these sources of bias on biological parameters and population structure can invalidate conclusions reached with any kind of production model used for stock management and assessment.

EGG MORTALITY OF THE PERUVIAN ANCHOVY (*Engraulis ringens*) CAUSED BY CANNIBALISM AND PREDATION BY SARDINES (*Sardinops sagax*)*

by

H. Santander[1]
J. Alheit[2]
A.D. MacCall[3]
A. Alamo[1]

[1] Instituto del Mar del Peru, Apartado 22, Callao-Peru

[2] Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA), IMARPE, Apartado 22, Callao-Peru

[3] Southwest Fisheries Center, P.O. Box 271, La Jolla-CA. 92038, U.S.A.

* Publication No. 8 of PROCOPA

Resumen

En Agosto-Septiembre 1981, se colectaron 925 muestras de ichthyoplancton, y estómagos de 1 500 anchovetas (*Engaulis ringens*) y 578 sardinàs (*Sardinops sagax sagax*); estas muestras fueron colectadas de una extensión de 600 millas a lo largo de la costa peruana entre los 6°S y 14°S. Los análisis de las muestras de plancton revelaron que los huevos de anchoveta estaban concentrados en una franga relativamente angosta, de alrededor de 9 millas de ancho, pararela a la costa y a una distancia de 8 a 17 millas de ésta. Los huevos no parecen ser transportados muy lejos de las áreas de desove. La tasa diaria de mortalidad de los huevos de anchoveta es extremadamente alta: 60% ($Z = 0.91$). Las anchovetas consumen más huevos en las áreas donde la densidad de huevos es alta y se alimentan menos de estos cuando la densidad de huevos es baja. El 61.1% de los estómagos de anchoveta y el 62.4% de los estómagos de sardina contenían huevos de anchoveta. El número promedio de huevos de anchoveta en los estómagos de anchoveta fue de 5.5, y en los estómagos de sardina fue de 16.4. Los huevos de edades diferentes parecen ser digeridos a ritmos diferentes. La predación de sardinas sobre huevos de anchoveta puede ser particularmente peligrosa ahora que el stock peruano de anchoveta ha alcanzado el nivel más bajo que jamás se haya registrado. Una comparación entre la anchoveta peruana y la anchoveta del norte frente a California (*E. mordax*) muestra que la contribución del canibalismo de huevos a la mortalidad total de los huevos es mayor en la anchoveta del norte.

INTRODUCTION

Predation on eggs either by cannibalism or by other species might regulate the size of fish stocks. Recently, egg cannibalism in the northern anchovy, *Engraulis mordax*, was the subject of a detailed investigation (Hunter and Kimbrell, 1980; MacCall, 1980). It was concluded that cannibalism on eggs and larvae is sufficiently intense to be a regulatory mechanism.

Egg cannibalism in the Peruvian anchovy, *E. ringens*, has been recorded several times (Rojas de Mendiola and Ochoa, 1973; Rojas de Mendiola, 1980). However, sample sizes were too small to draw firm conclusions. Furthermore, important parameters, e.g., egg mortality, batch fecundity, spawning rate, etc., were not known and, consequently, the impact of egg cannibalism could not be estimated.

In 1981, the Instituto del Mar del Perú, carried out a cruise to estimate the spawning biomass of the central and northern anchovy stock. The samples and data obtained from this cruise gave the opportunity to estimate the extent of egg cannibalism in the Peruvian anchovy and to determine the effect of predation on anchovy eggs by sardines, *Sardinops sagax sagax*. Further details on biological parameters used in this study on egg cannibalism are given in Santander et al. (in prep.) and Alheit et al. (in prep.). This investigation was a cooperative effort of IMARPE and the Peruvian-German Fisheries Research Project which was financed by the German Agency of Technical Cooperation (GTZ).

METHODS

In August/September 1981, 925 ichthyoplankton samples were collected by the R/V 'Humboldt' along the Peruvian coast from Pisco in the south to Punta Falsa in the north. Vertical hauls from 70 m. were carried out with the Calvet net. The area under investigation was divided up into three regions: Region 1, from Punta Falsa to Salaverry, Region 2, from Salaverry to Puerto Supe and Region 3, from Puerto Supe to Pisco. More details on the egg samples from the sea are given in Santander et al. (in prep.).

With a delay of one to two weeks, 50 collections of anchovies and 16 collections of sardines, each one consisting of about 30 fish, were taken in the same area by a purse-seiner. The body cavity of the fish was opened and they were preserved in 10% formalin.

Anchovy eggs were assigned to three different age phases according to their embryonic development. Phase 1 corresponds to stages 1-2 of Santander and O.S. de Castillo (1973), phase 2 corresponds to stage 3-11 and phase 3 corresponds to stage 12-18.

RESULTS

Comparison of the abundances of eggs in the sea and of eggs encountered in stomachs. Anchovy eggs occurred along the whole Peruvian coastline from the north, about midway between Punta Falsa and Pimentel, down to the south, to Tambo de Mora (Figure 1). High densities (more than 100 eggs per sample = 0.05 m^2) were recorded opposite Chicama, Salaverry, Chimbote, Huarmey, Puerto Supe, Huacho, Ancón, Callao and Tambo de Mora. The highest densities were around 1,000 eggs per sample, i.e., 20,000 eggs per m^2. The mean numbers of anchovy eggs per anchovy stomach are included in Figure 1.

There is good agreement between the positions of collections with high numbers of eggs per stomach and the high densities of anchovy eggs in the sea, particularly opposite Chicama, Salaverry, Huacho, Ancón and Callao. Only one collection out of 50 did not have any anchovy with anchovy eggs in the stomach, and this collection was taken outside of the distribution area of the anchovy eggs in the sea. The distribution of the sardine eggs along the coast was not continuous, as it was in the case of the anchovy, but rather patchy (Figure 2). Again, the correspondence of occurrence of sardine eggs in the sea with the occurrence of sardine eggs in anchovy stomachs was fairly good, apart from the northern area. However, it has to be taken into account that the stomach samples were

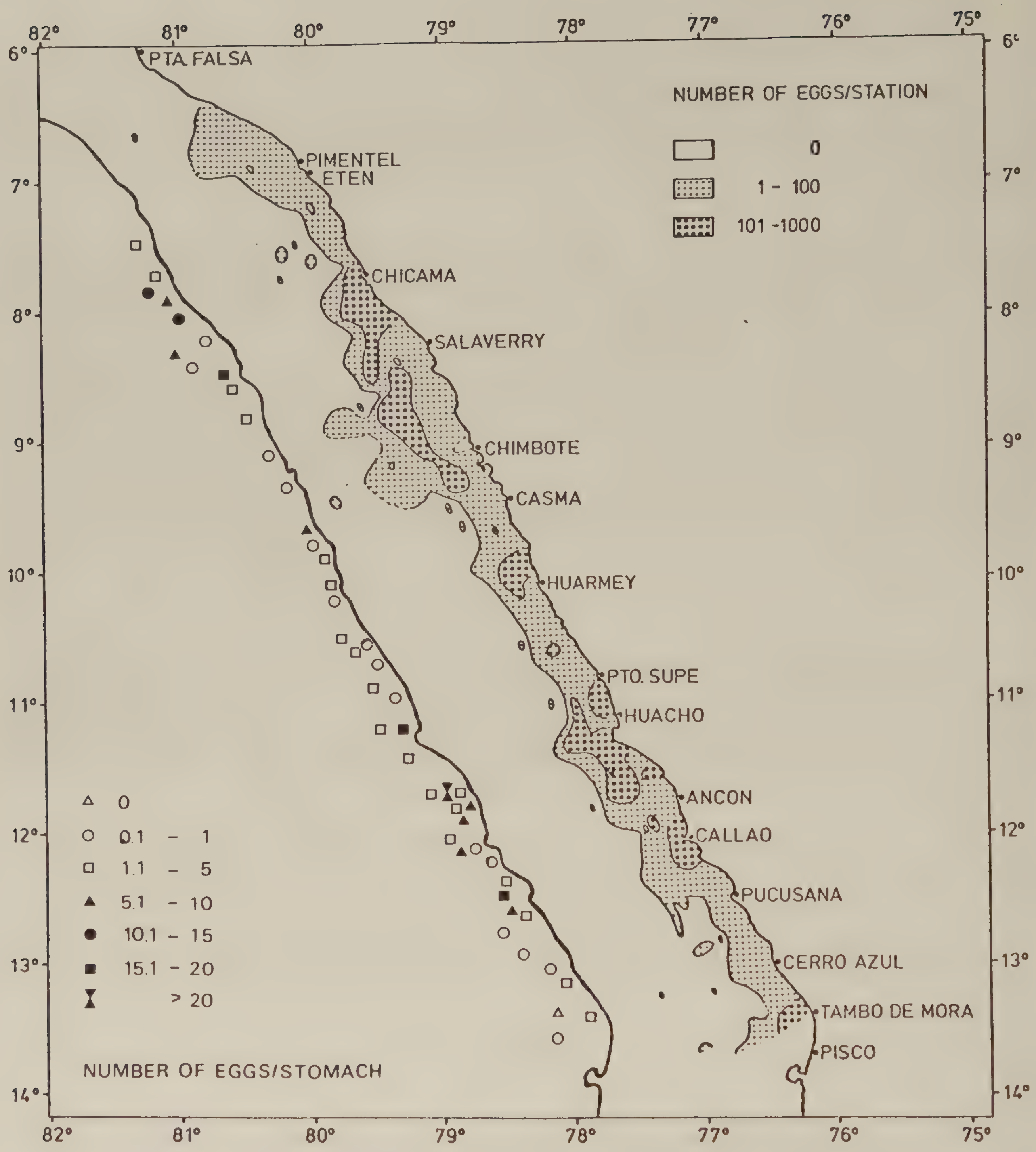

82°
81°
80°
79°
78°
77°
76°
75°
6°
7°
8°
9°
10°
11°
12°
13°
14°
PTA. FALSA
PIMENTEL
ETEN
CHICAMA
SALAVERRY
CHIMBOTE
CASMA
HUARMEY
PTO. SUPE
HUACHO
ANCON
CALLAO
PUCUSANA
CERRO AZUL
TAMBO DE MORA
PISCO
NUMBER OF EGGS/STATION
0
1 - 100
101 -1000
△ 0
○ 0.1 - 1
□ 1.1 - 5
▲ 5.1 - 10
● 10.1 - 15
■ 15.1 - 20
⧗ > 20
NUMBER OF EGGS/STOMACH

Fig. 1. Distribution and densities of anchovy eggs in the sea and in anchovy stomachs.

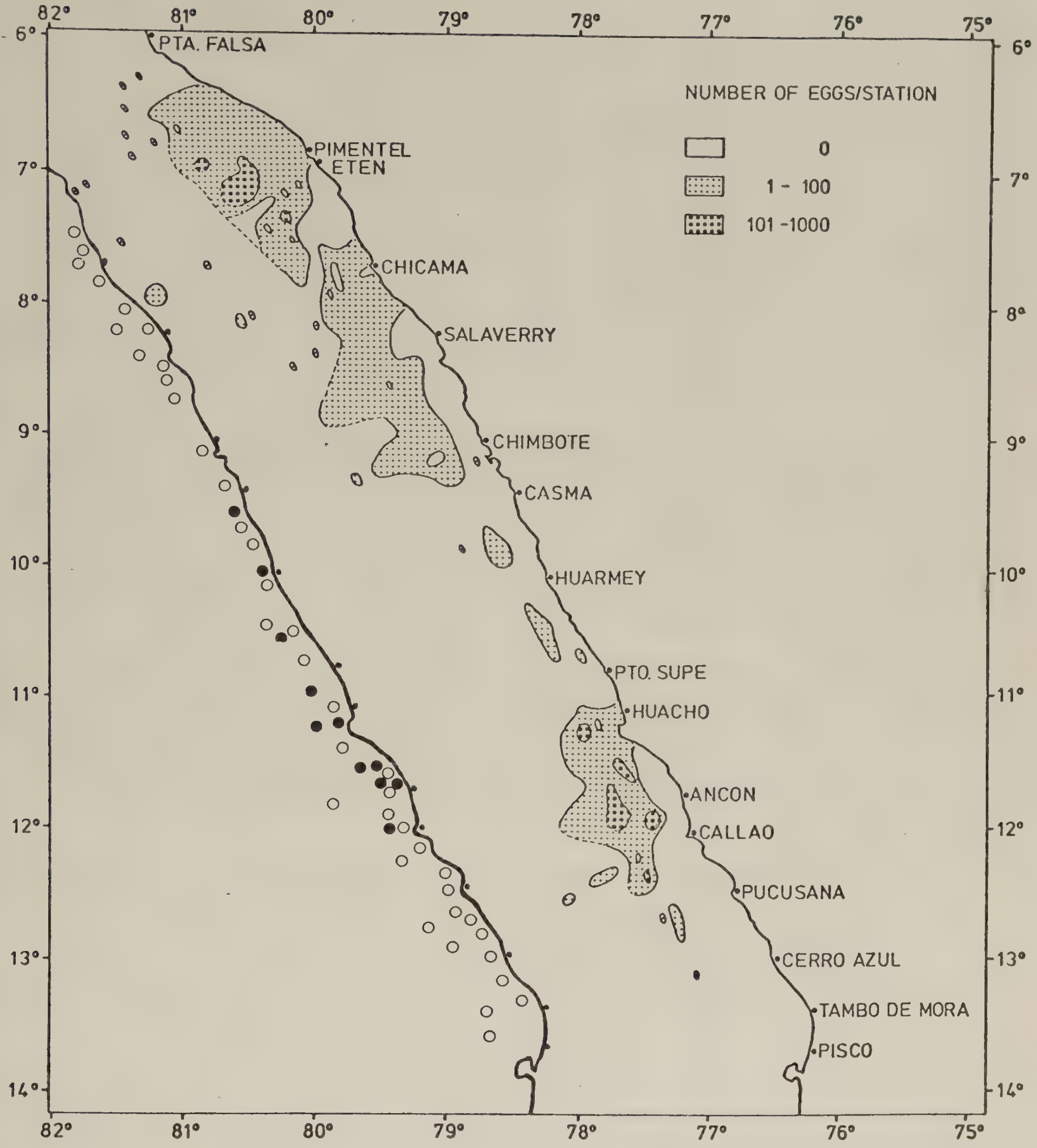

82°
81°
80°
79°
78°
77°
76°
75°
6°
7°
8°
9°
10°
11°
12°
13°
14°
PTA. FALSA
PIMENTEL
ETEN
CHICAMA
SALAVERRY
CHIMBOTE
CASMA
HUARMEY
PTO. SUPE
HUACHO
ANCON
CALLAO
PUCUSANA
CERRO AZUL
TAMBO DE MORA
PISCO
NUMBER OF EGGS/STATION
0
1 - 100
101 -1000

Fig. 2. Distribution of sardine eggs in the sea and in anchovy stomachs. ● = sardine eggs found in stomachs, ○ = no sardine eggs found in stomachs.

collected about one to two weeks later than the egg samples. This explains why there is not much correspondence in some areas and it demonstrates that some spawning areas are rather stable over a period of one to two weeks.

Maximum densities of anchovy egg distribution. The density peaks of anchovy eggs were encountered at different distances off the coast in the three regions (Figure 3). In Region 1, in the north, the highest densities were between 8 and 14 miles off the coast. In Region 3, in the south, the highest densities were between 11 and 17 miles off the coast. However, in the middle, in Region 2, high densities were encountered over a large area, from 8 to 29 miles off the coast. When the data of the three regions are combined, it becomes evident that the highest densities were encountered from 11 to 14 miles off the coast, and that still fairly high densities were at 8 and 17 miles. The sites of the collections with high numbers of eggs per stomach partly overlap with the sites of high densities of anchovy eggs in the sea (Figure 4): With one exception, all collections with a mean value of more than 4 eggs per stomach were collected between 5.2 and 15.6 miles off the coast. This demonstrates that the anchovies take up more eggs in areas of high egg densities and eat less eggs in areas of lower densities.

Distribution of eggs in different phases of embryonic development. From Figure 3, it was assumed that the eggs are spawned by the anchovies mainly between 8 and 17 miles off the coast and that the eggs are then transported offshore and inshore. The decrease of egg densities offshore and inshore was supposed to be caused by a dilution effect due to transportation by water movements and due to a high egg mortality. The period from the spawning of the egg to the hatching of the larva is temperature dependent and lasts in the Peruvian anchovy about 2 to 2.5 days (Santander et al., in prep.). It was expected to find young newly spawned eggs mainly in the areas of high egg densities, whereas older eggs should be encountered further inshore and, particularly, further offshore.

To study these processes, the eggs collected from the sea and from the stomachs were assigned to three phases according to the state of their embryonic development (Table 1). The distribution of the three age phases was studied separately for the three regions. In doing that, one has to be aware of the fact that the duration of the three age phases is very different. Thus, e.g. the number of eggs in phase 1 should be relatively low, because this phase lasts only about 2.4 hours at 16.5°C. In Region 1 (Figure 5) the peak of phase 1 eggs was at 17 miles off the coast. Phase 2 peaked further inshore, at 11 and 14 miles. Phase 3 had its peak at 17 miles as phase 1.

Table 1: Duration of egg phases at 16.5°C, modified after P.E. Smith (MS, 1982).

Phase	Duration (h)
1	2.4
2	28.5
3	25.3

This demonstrates that the majority of the eggs is not transported away very far from the site of their spawning. However, with increasing age of the eggs the density peaks are less pronounced and older eggs seem to be spread more evenly over the area under investigation. Similar distributional movements of eggs in different phases took place in Region 2 (Figure 6) and Region 3 (Figure 7). In all three regions, the density peaks of phase 1 and phase 3 correspond with each other exactly, whereas the peak of phase 2 is always further inshore or offshore.

For the area between 5 and 23 miles offshore, the percentages of the eggs in the three phases were calculated (Table 2). 7.2% to 19.4% of the eggs were in phase 1, 68.6% to 86.8% in phase 2 and 6.0% to 12.0% in phase 3. On average, 13.4% of the eggs were in phase 1, 78.5% in phase 2 and 8% in phase 3. The same procedure was carried out with the eggs obtained from the stomachs. However, in this case, 39% of the eggs were in phase 1, 37% in phase 2 and 23.7% in phase 3. That means, about three times as many eggs as supposed were in phase 1 and 3, whereas only about the half of that what was expected was in phase 2.

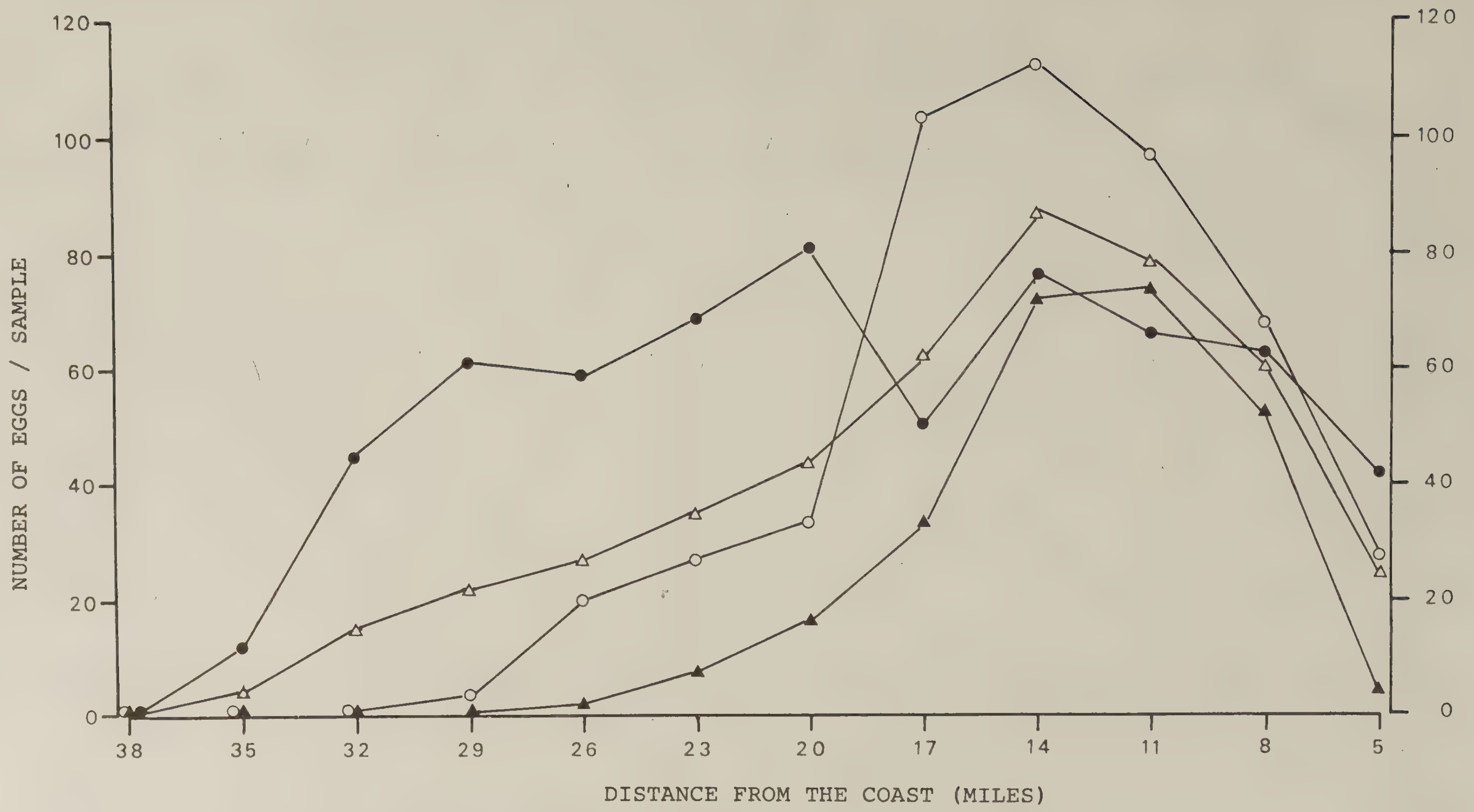


Fig. 3. Anchovy egg densities and their distance from the coast.
△ = Total area, ▲ = Region 1, ● = Region 2, ○ = Region 3.

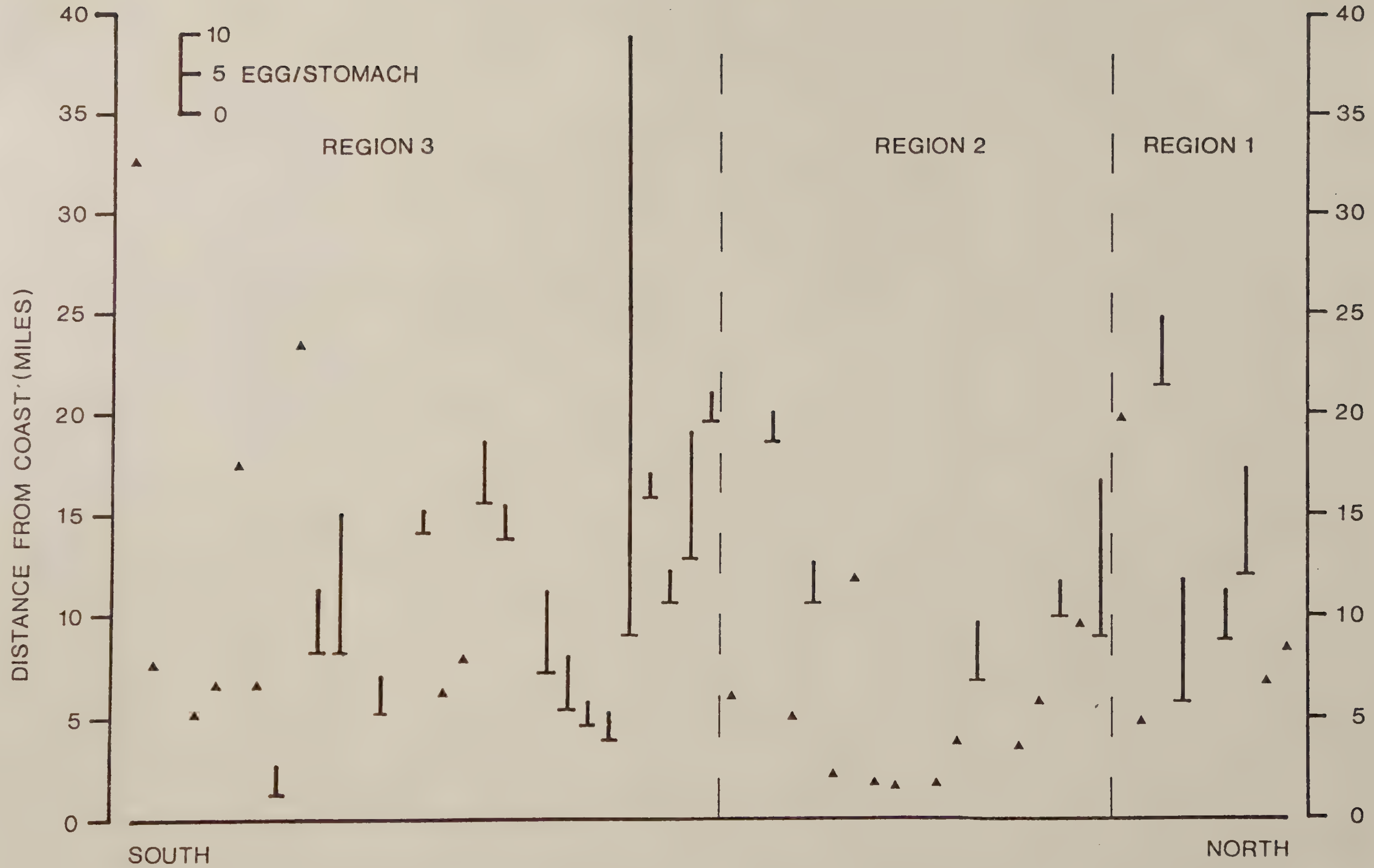


Fig. 4. Distance of anchovy collections from coast and mean number of eggs in anchovy stomachs per collection. ⊥ = indicates in which distance from the coast the collection was taken, ▲ = less than four eggs per stomach.

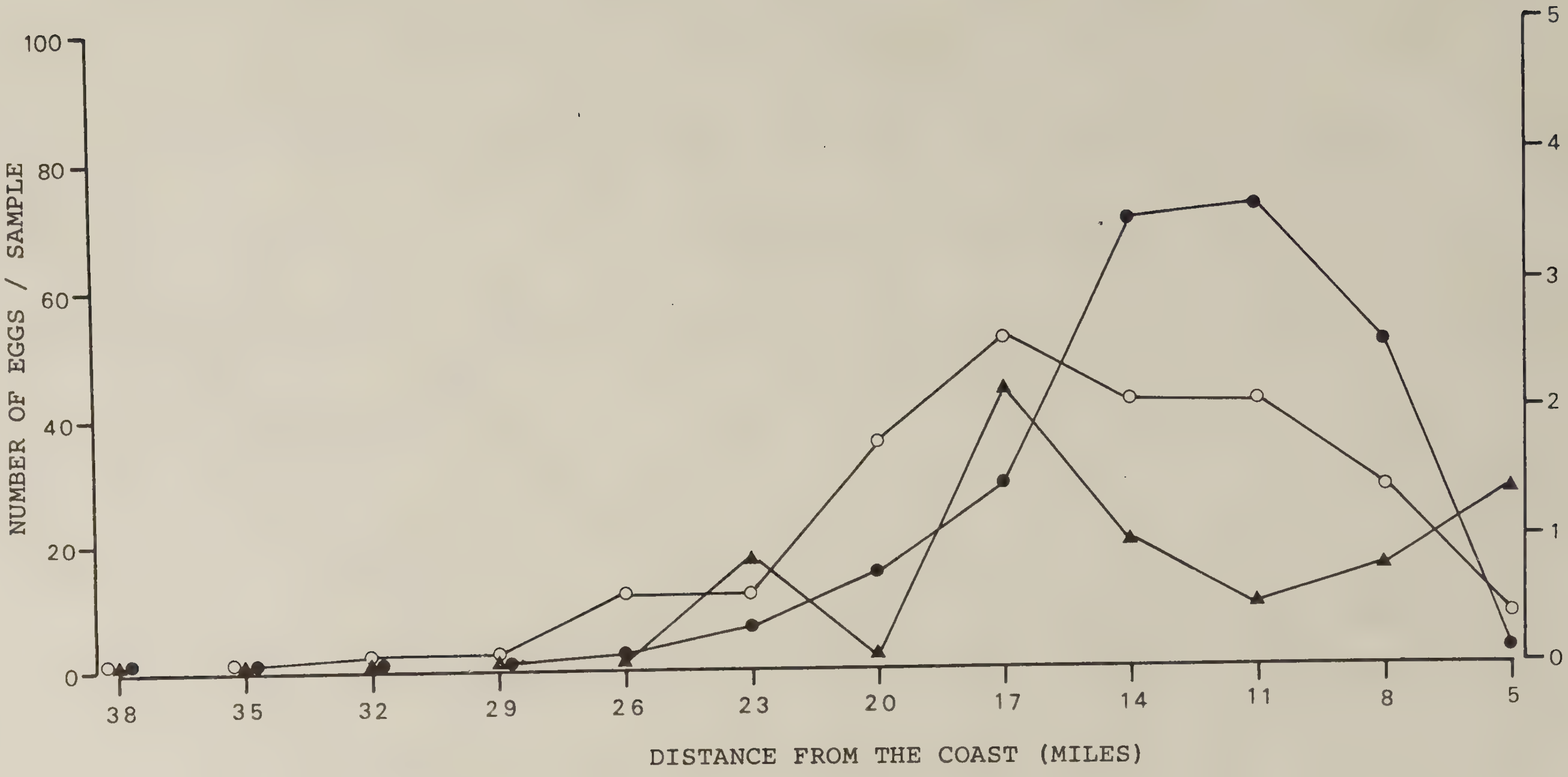


Fig. 5. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 1. ▲ = Phase 1, ● = Phase 2, ○ = Phase 3.

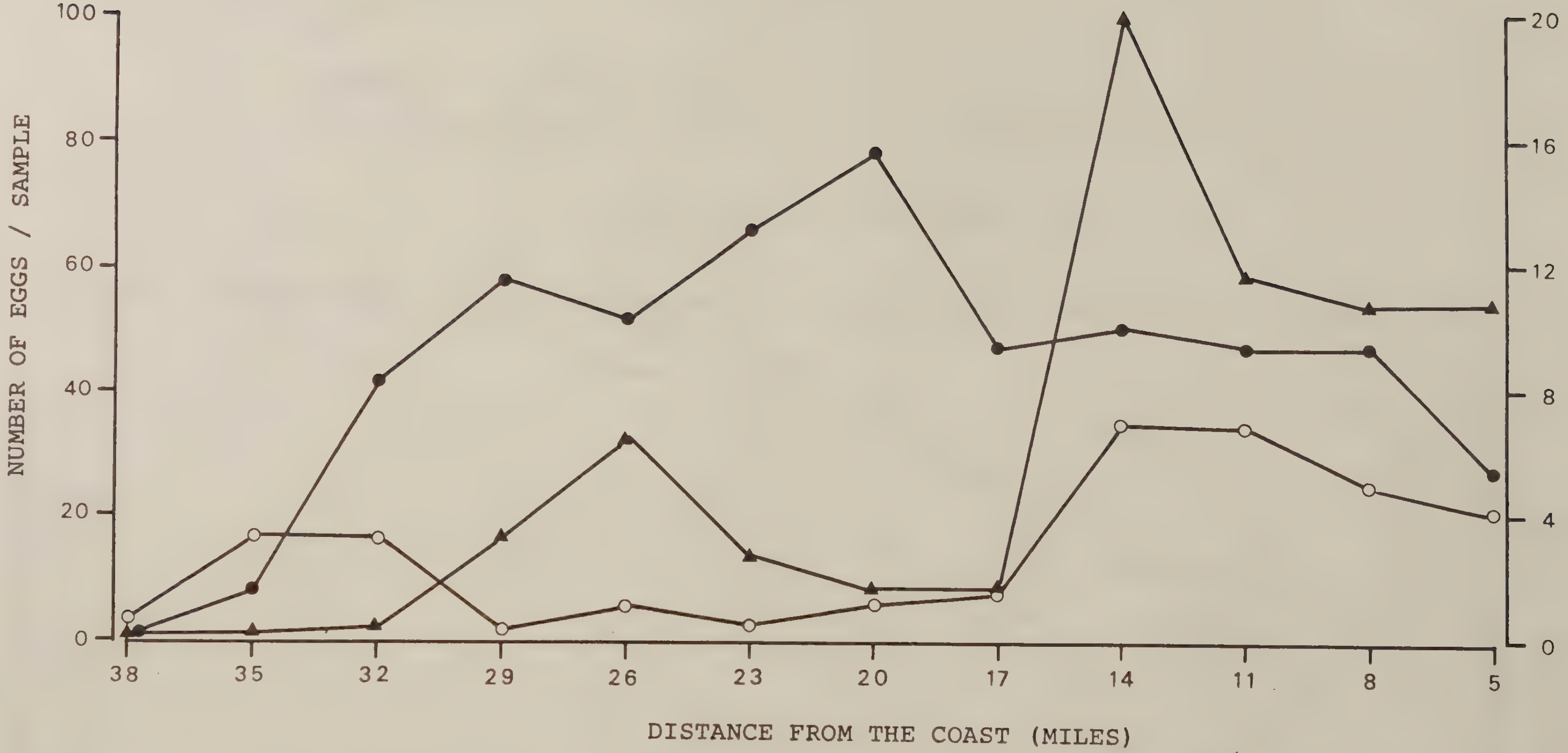


Fig. 6. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 2.

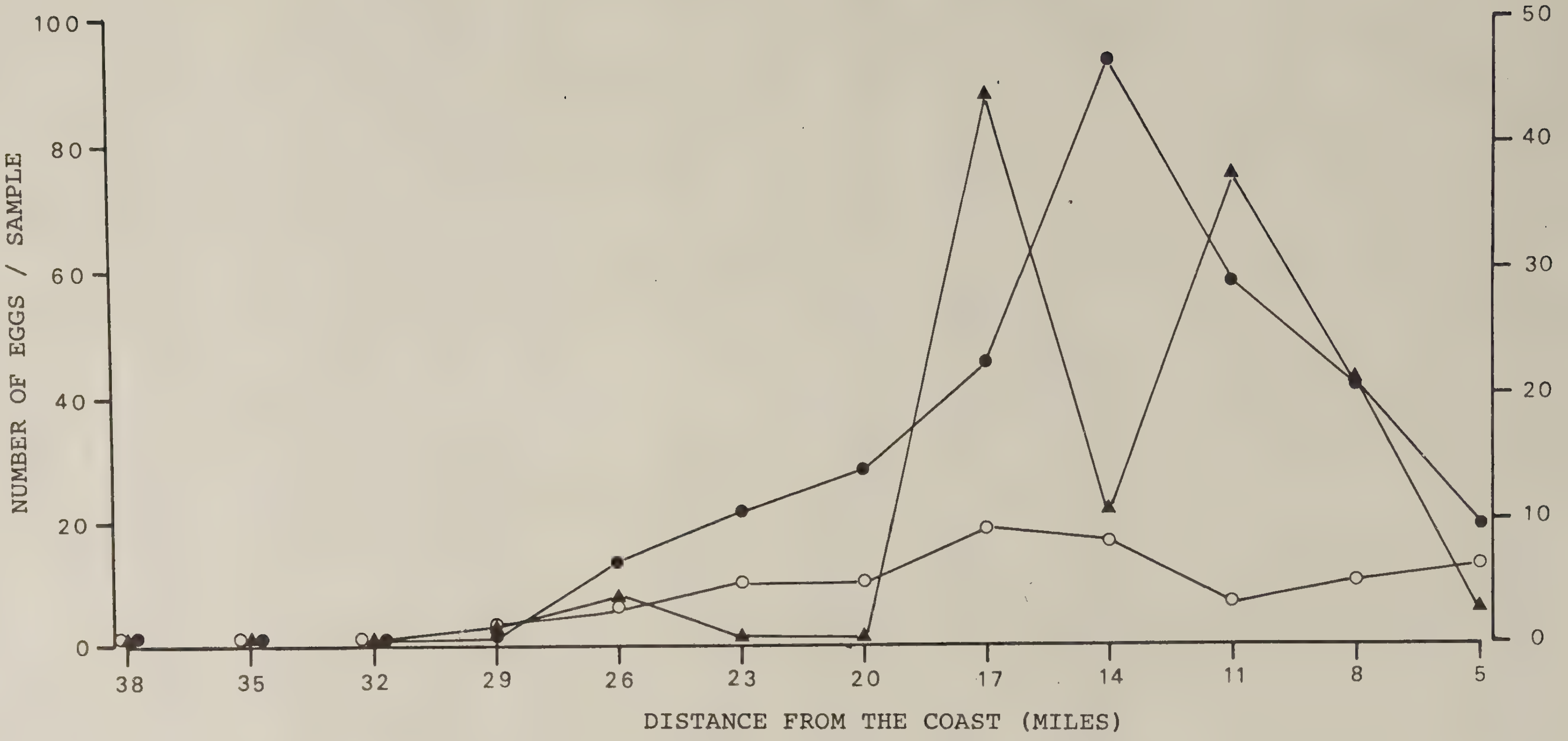


Fig. 7. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 3.

Table 2: Percentages of eggs in phase 1, 2, and 3. For the eggs collected from the sea, only the area between 5 - 23 miles offshore was considered. The total percentage of the eggs in the stomachs was calculated from all collections of stomachs.

Region	Phase 1		Phase 2		Phase 3	
	Sea	Stomach	Sea	Stomach	Sea	Stomach
Region 1	7.2	69.2	86.8	17.8	6.0	13.0
Region 2	13.7	13.6	80.2	53.3	6.1	33.1
Region 3	19.4	39.2	68.6	37.2	12.0	23.7
TOTAL	13.4	39.3	78.5	37.0	8.0	23.7

Phase 1, which lasts only about 2.4 hours at a temperature of 16.5°C, is not only overrepresented in the stomach contents, but it is encountered as well in stomachs which were collected a long time after phase 1 had disappeared from the sea. The daily spawning period starts usually at 18.00 hours at night and lasts until 02.00 hours in the morning. (Santander et al., in prep.). After 05.00 hours in the morning, phase 1 eggs should not be anymore in the sea. However, phase 1 eggs were obtained from stomach samples which were taken at any time over the daily 24 hours cycle (Table 3). The percentages of phase 1 eggs in stomachs were particularly high in the morning hours and they dropped towards the late afternoon, but phase 1 eggs did not disappear totally from the stomachs at any time of day.

Table 3: Percentages of eggs in phase 1, 2, and 3. Recovered from stomachs which were collected at different times of day. Each collection had 30 anchovies.

Time of day (hours)	Number of Collections	% of eggs		
		Phase 1	Phase 2	Phase 3
07.00-10.59	11	58.5	24.5	17.0
11.00-14.59	7	53.1	32.1	14.7
15.00-18.59	9	14.8	53.9	31.3
19.00-22.59	10	30.7	38.9	30.4

Comparison of mean numbers of anchovy eggs in anchovy and sardine stomachs. A total of 1,500 anchovy stomachs from 50 collections each one containing 30 fish were analysed for numbers of anchovy eggs. Mean numbers of eggs per stomach in these 50 collections ranged from 0 to 79.4 eggs. The total mean was 5.5 anchovy eggs per anchovy stomach (Table 4). A total of 578 sardine stomachs from 16 collections each one containing on average 36 fish were analysed, too. Mean number of anchovy eggs per stomach in these 16 collections ranged from 0 to 120.0 per sardine stomach. The total mean was 16.4 anchovy eggs per sardine stomach (Table 4). According to these data, an individual sardine had about three times as many anchovy eggs in its stomach than an anchovy.

Table 4: Number of collections, total number of stomachs analysed, percent of stomachs with eggs and mean number of eggs per stomach in anchovies and sardines.

	Anchovies	Sardines
Number of collections	50	16
Total number of stomachs	1,500	578
Stomachs with anchovy eggs, %	61.1	62.4
Mean number of eggs per stomach	5.5	16.4

Calculation of percentage natural egg mortality from egg cannibalism. Hunter and Kimbrell (1980) calculated how much natural mortality is due to egg cannibalism. Their method was slightly modified by MacCall (1980) who used the catch equation to determine the coefficient of mortality due to cannibalism:

$$F_c = \frac{C_c}{E_o} x \frac{Z}{1-e^{-Zt}}$$

Where:

C_c = daily egg consumption per gram of adults

E_o = daily egg production per gram of adults

F_c = coefficient of mortality due to cannibalism

Z = coefficient of total mortality

t = length of time eggs are subject to mortality (i.e., time from spawning to hatching).

Using Hunter and Kimbrell's (1980) method and including MacCall's (1980) modification, the percentage of mortality due to egg cannibalism was calculated for the Peruvian anchovy and compared to that of the northern anchovy (Table 5). Whereas in Peru, egg cannibalism was responsible for 10% of the total egg mortality, this value was 28% for the northern anchovy.

Table 5: Estimation of the percentage of natural egg mortality due to egg cannibalism in Peruvian and northern anchovy. The sources of the data for the Peruvian anchovy are Santander et al. (in prep.) and for the northern anchovy Hunter and Kimbrell (1980) and MacCall (1980). The variables B, C and H in the estimation for the Peruvian anchovy come from Hunter and Kimbrell (1980).

Variable	Peruvian Anchovy	Northern Anchovy
A Mean eggs/stomach	5.5	5.1
B Rate of gastric evacuation	.701	.701
C Duration of feeding (h)	24	24
D Ration, eggs/fish	92.53	85.80
E Mean fish weight (g)	25.8	16.8
F Ration, eggs/grams wet weight = C_c	3.6	5.1
G Eggs spawned/grams ovary-free female weight	581	389
H Ratio of ovary-free weight to total female weight	.954	.954
I Eggs spawned/grams total female weight	554	371
J Ratio of females spawning/night	.16	.16
K Ration of females/school	.5	.5
L Eggs/gram school weight = E_o	44.4	29.7
M Coefficient of natural egg mortality = Z	.91	.39
N Length of time eggs are subject to mortality = t	2.0	2.5

DISCUSSION

At the present state of knowledge, it is difficult to explain why eggs of phase 1 and 3 are overrepresented in anchovy stomachs. Misidentification is clearly not the reason, as eggs of the three phases cannot be confused with each other. All eggs which could not be identified were labelled as 'disintegrated' and not included in the calculations. However, it might be that eggs of phase 2 are particularly vulnerable to 'disintegration' in anchovy stomachs. Furthermore, as not much is known about the vertical distribution of anchovy eggs in different stages of embryonic development, it could be argued that phase 2 eggs are in depths in which the anchovies feed less. However, that does not seem very probable.

Another puzzle is the occurrence of phase 1 eggs in fish stomachs collected in the late afternoon. The analysis of the egg samples from the field demonstrated clearly that spawning is terminated at 02.00 hours and that no spawning takes place in daytime. The only explanation is that phase 1 eggs encountered in fish stomachs collected in the late afternoon must have been fed upon a long time before the fish were collected. That means, they must have spent several hours in the fish stomachs without being affected much by digestive processes. Hunter and Kimbrell (1980) report that identifiable parts of eggs may remain in the stomachs up to 8 hours, but the contents of the eggs (embryo and yolk) are digested after 2 hours. As the content of phase 1 eggs from stomachs collected in the afternoon was not damaged, one may conclude that phase 1 eggs are particularly resistant towards digestive processes. This supports the above mentioned hypothesis of differential vulnerability to 'disintegration' of eggs in different age phases.

The data in Table 5, give the impression that egg cannibalism in anchovies plays a less important role in the Peruvian anchovy. This would be surprising as the egg densities in the Peruvian ecosystem are higher than in the Californian system (Santander et al., 1982). However, it has to be considered that different methods were applied to collect the fish. Whereas, in California, the fish were caught with a trawl, in Peru, the anchovies were sampled with a purse-seiner. A purse-seine haul lasts usually 2 to 3 hours. If the fish stop feeding when the haul begins, a high number of eggs might already be digested by the time the fish are fixed in formalin. According to the gut evacuation rate determined in the laboratory by Hunter and Kimbrell (1980), the mean residence time of eggs in the stomach is only 1.4 hours. The 10% contribution of cannibalism to the total egg mortality estimated for the Peruvian anchovy (Table 5) has therefore, to be considered only as a minimum estimate.

For a long time, it has been speculated that exploited clupeoid species might be suppressed by competitors feeding on eggs and larvae (e.g. Murphy, 1977). The data on sardines predating on anchovy eggs which are presented here support this hypothesis. The mean number of anchovy eggs in sardine stomachs is more than three times higher than in anchovy stomachs (Table 4). However, it is not possible yet to estimate the consumption of anchovy eggs by sardines, as the stock size of the sardines in the spawning area of the anchovy is not known. Predation on anchovy eggs by sardines might be particularly dangerous to the central and northern Peruvian anchovy stock now, as the sardine stock seems to have been increasing over the last years (J. Valdivia, pers. comm.) whereas the anchovy stock has reached its lowest level ever recorded (Santander et al., in prep.).

REFERENCES

Alheit, J., V.H. Alarcon and B.J. Macewicz. (in prep.). Spawning rate and sex ratio in the Peruvian anchovy, Engraulis ringens.

Hunter, J.R. and C.A. Kimbrell. 1980. Egg cannibalism in the northern anchovy, Engraulis mordax. Fish Bull.(U.S.) 78:811-816.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as Engraulis. pp. 201-220. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes. (G.D.Sharp, ed.) Intergovernmental Oceanographic Commission, Workshop Report 28. IOC/UNESCO, Paris.

Murphy, G.I. 1977. Clupeoids. pp. 283-308. In Fish Population Dynamics (J.A. Gulland, ed.) John Wiley and Sons New York. 372 p.

Rojas De Mendiola, B. 1980. Summary of the studies about food and feeding habits of the anchovy (Engraulis ringens J.) pp. 221-231. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes. (G.D. Sharp, ed.) Intergovernmental Oceanographic Commission, Workshop Report 28. IOC/UNESCO, Paris.

Rojas de Mendiola, B. and N. Ochoa. 1973. Observation on the food and feeding habits of the anchovy Engraulis ringens (Jenyns) made during cruise 6908-09. pp. 457-461. In Oceanography of the south Pacific (R. Fraser, comp.) New Zealand Nat.Comm.for UNESCO, Wellington, New Zealand.

Santander, H. y O.S. de Castillo. 1973. Estudio sobre las primeras etapas de vida de la anchoveta. Inf.Inst.Mar.Peru, Callao. 41:3-30.

Santander, H., J. Alheit and P.E. Smith (in prep.). Estimacion de la biomasa desovante de la anchoveta Peruana, Engraulis ringens, del stock central y norte en 1981 usando el 'Metodo de Producción de Huevos'. Bol.Inst.Mar.Peru, Callao.

Santander, H., P.E.Smith and J. Alheit. 1982. Determination of sampling effort required for estimating egg production of anchoveta, Engraulis ringens, off Peru. Bol.Inst.Mar. Peru, Callao. 7:3-18.

COMPARISON OF EGG SAMPLE PROBABILITY DISTRIBUTIONS OF THE ANCHOVY (*Engraulis ringens*) AND SARDINE (*Sardinops sagax*) OFF PERU AND THE ANCHOVY (*Engraulis mordax*) AND THE SARDINE (*Sardinops caerulea*) OFF CALIFORNIA

by

Paul E. Smith,[1] Haydee Santander[2] and Jürgen Alheit[3]

[1]Southwest Fisheries Center
P.O. Box 271
La Jolla, CA 92038
USA

[2]Instituto del Mar del Perú
Esq. Gamarra y Gral. Valle
Apartado Postal 22
Chucuito, Callao
Perú

[3]Programa Cooperativo Peruano-Alemán de
Investigación Pesquera (PROCOPA)
Instituto del Mar del Perú
Esq. Gamarra y Gral. Valle
Apartado Postal 22
Chucuito, Callao
Perú

Resumen

Se dispone de datos de reconocimiento de ictioplancton de más de 20 años del sistema de afloramiento del Perú y de más de 30 años del sistema de afloramiento de California. Se comparan las distribuciones de probabilidad de muestras de huevos de dos especies de clupeidos de estos dos sistemas (*Engraulis ringens* y *Sardinops sagax* del Perú y *E. mordax* y *S. caerulea* de California). El análisis de las distribuciones de las muestras de huevos combinado con datos adicionales permite estudiar actividades biológicas importantes de peces pelágicos, tales como agregación, fertilización, etc. Además se puede determinar la efectividad de canibalismo directo e incidental, de la predación, y de otras causas de mortalidad a través de la distribución inicial de huevos y la dispersión subsiguiente y el transporte hacia afuera de las áreas de desove. La escala e intensidad del patrón cambian con el tiempo y pueden afectar el esfuerzo de muestreo que se requiere para estimar la producción y sobrevivencia de los huevos y pueden complicar el ajuste de las ecuaciones de mortalidad que asumen una varianza constante con términos absolutos o relativos.

INTRODUCTION

The egg sample probability distribution of the Peruvian anchovy (*Engraulis ringens*) has been used to design an egg production survey with precision estimated from existing samples by Santander, Smith, and Alheit (1982). It should be possible, with existing data, to estimate the optimum survey effort for the determination of egg production of the sardine off Peru and California and analagous multiple pelagic-spawners of other species and in other areas, given historical sample data.

It is the purpose of this paper to briefly compare historical data on egg abundance per sample for four stocks from two genera (*Engraulis* and *Sardinops*), from two habitats (Peru and California). While it is not yet possible to infer historical egg production rates from these sets of data it should now be possible to estimate the number of samples needed for a given precision in future surveys. Also the analysis of sample probability distributions may lead to new insights into the origins of patches of eggs and the fate of the spawning products as they disperse (Smith,1973) and the causes and degree of variation in the survival of the spawning products. This study was part of a cooperative project of the Southwest Fisheries Center, California, the Instituto del Mar del Peru and the "Cooperative Peruvian-German Fisheries Research Project" (PROCOPA) which is financed by the "German Agency of Technical Cooperation" (GTZ).

METHODS

Detailed accounts of sampling and sorting methods are given by Santander and S. de Castillo (1979) for the Peruvian samples and by Kramer et al. (1972) for the Californian samples. Briefly, the IMARPE samples are from a Hensen Egg Net towed vertically from 50 meters depth sampling directly under 0.3 square meters. The CalCOFI samples were towed obliquely from 140 or 210 meters. To report the values in similar units the IMARPE samples are divided by 3 and both are reported here as eggs per square meter sea surface area.

RESULTS

The number of anchovy eggs in the IMARPE samples was greater than the number of anchovy eggs in the CalCOFI samples. The number of sardine eggs in the IMARPE samples was greater than those in the CalCOFI samples. Both species of the genus *Engraulis* yielded number of eggs greater than the cohabitant of the genus *Sardinops* (Figures 1 and 2).

Part of the differences between the numbers of eggs per sample are due to the sampling technique. Some anchovy eggs are lost through the meshes of the CalCOFI net. Also the lower treshhold of egg density detected by the IMARPE net is higher (3 eggs per square meter) than that detected by the CalCOFI net (approximately 0.3 eggs per square meter). Since the bulk of the population at the egg stage is in the larger samples, it is not likely that these differences will be important.

The difference in sardine eggs per unit surface area between IMARPE samples and CalCOFI samples is of the same order of magnitude as the difference in anchovy egg sample sizes. In both cases the difference is between 4- and 16-fold. This signals a radical difference between the Peruvian and Californian habitats which directly effects both sardine and anchovy at the time of spawning and during the subsequent dispersal and mortality phase.

DISCUSSION

The most important result of this study is that for a given precision it will be necessary to take more samples in the area of spawning to estimate the egg production of the stocks of *Engraulis* and *Sardinops* off Peru than off California. That this is not inherent in the different methods of sampling or different stock sizes is indicated by the stability of the egg distributions of the Californian sardine when several different samples sizes were used while the spawning biomass changed from 4 million tons to less than 10 thousand tons (Smith and Ricardson, 1977).

FIGURE 1

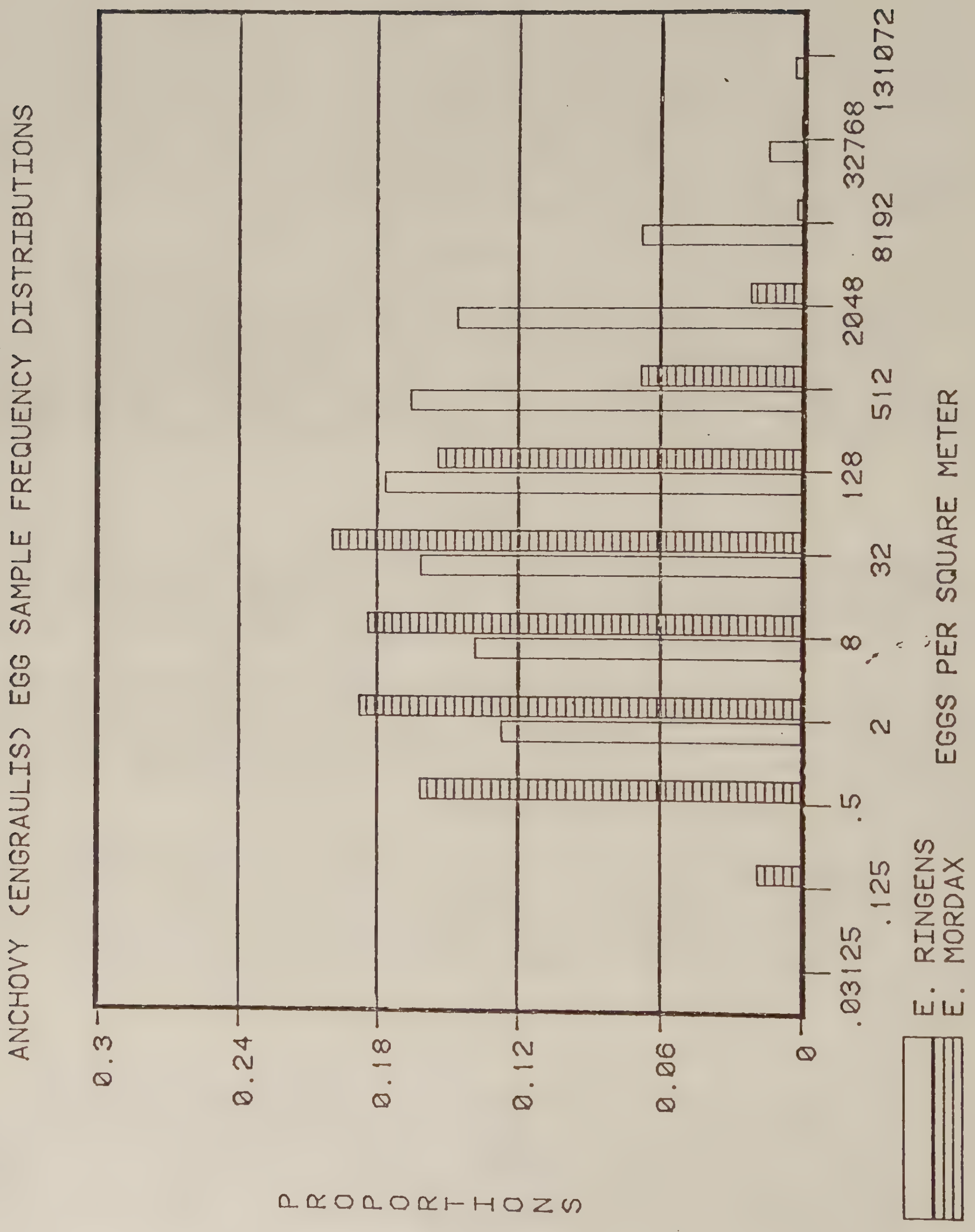
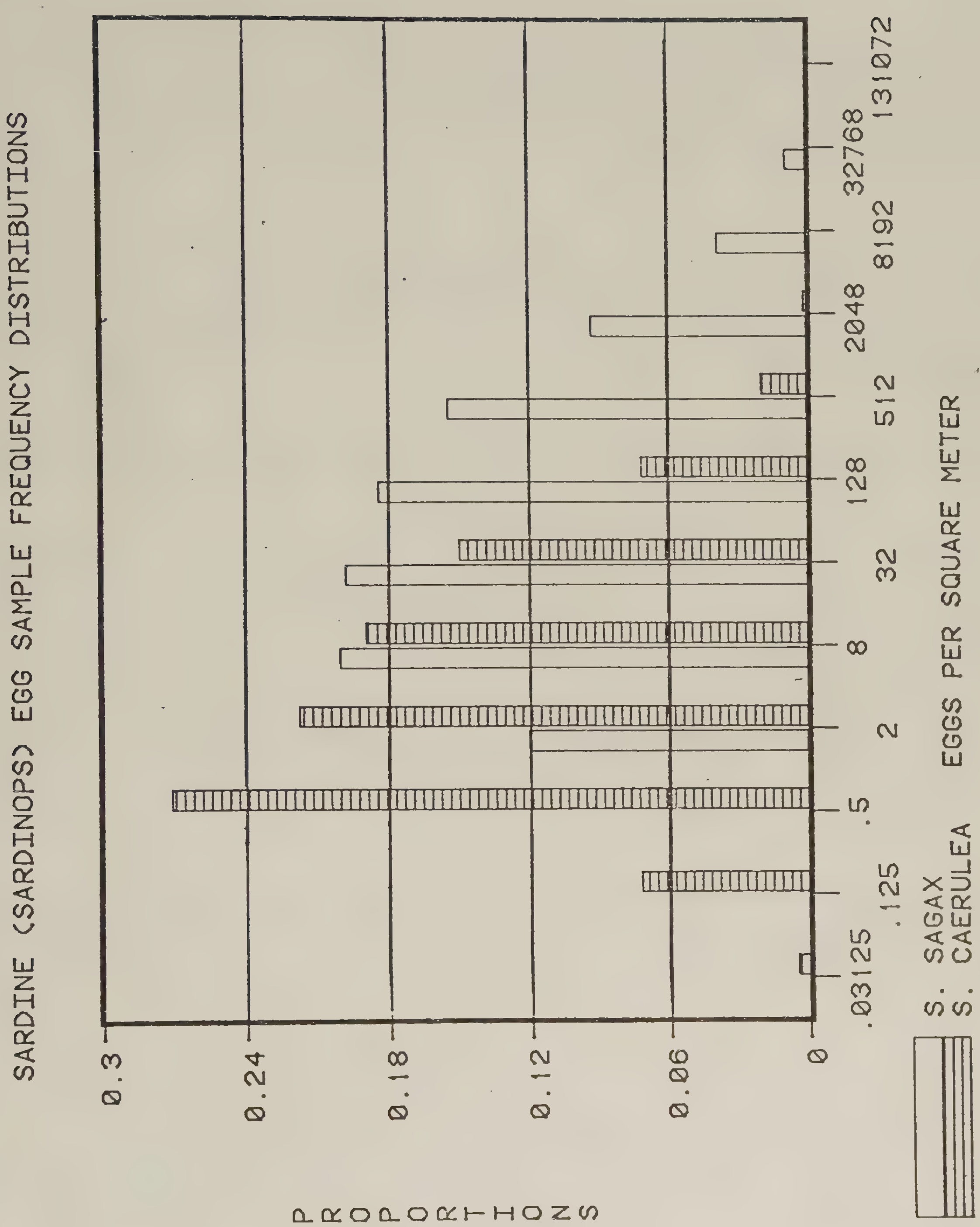

ANCHOVY (ENGRAULIS) EGG SAMPLE FREQUENCY DISTRIBUTIONS
PROPORTIONS
0.3
0.24
0.18
0.12
0.06
0
.03125
.125
.5
2
8
32
128
512
2048
8192
32768
131072
EGGS PER SQUARE METER
E. RINGENS
E. MORDAX

FIGURE 2


SARDINE (SARDINOPS) EGG SAMPLE FREQUENCY DISTRIBUTIONS
PROPORTIONS
0.3
0.24
0.18
0.12
0.06
0
.03125
.125
.5
2
8
32
128
512
2048
8192
32768
131072
EGGS PER SQUARE METER
S. SAGAX
S. CAERULEA

To explore the meaning of the egg sample distributions presented here, it is necesary to postulate a conceptual framework for the four stocks of fish which incorporates spatial distribution of mature adult fish at the time of spawning and the time distribution of the spawning process.

Spatial scale and intensity of distribution: Unfortunately the features of spatial scale and intensity are not equally well known for the four stocks examined here. The geographic distribution of all four species is well known. Also, the stock boundaries are well known in the offshore-onshore plane, but are less well known along the coast and these stock divisions may fluctuate with season and with interannual climatic conditions of changes in stock biomass (see MacCall, in prep.).

For scales of distribution below the species, and stock or subpopulation, only the beginning of perception has been reached for *Engraulis mordax*. Schools are unevenly distributed in the habitat and the aggregations of schools are called "school groups" or "shoal groups" (Fiedler, 1978). These can be characterized as 3000 schools in a 6 nautical mile (10 km) disc with 100 schools per square nautical mile. While most of the schools are small (15 m radius) most of the fish are in large schools (50 m radius). The school groups probably include all ages and sizes of fish but the schools probably consist of either "0" group or adult but not both.

Hewitt, Smith and Brown (1976) estimated that the schools contained 15 kilograms of mature fish per square meter of which some faction are ready to spawn each night. It is not known what fraction of males participate in spawning each night. The females spawn in the height of the spawning season each 6 to 8 nights (Hunter and Macewicz, 1980; Alheit et al., this volume). That the spawners for a given night segregate within the school before spawning is suggested by the odd sex ratios (3 or 4 males per female) and above average proportions of spawning females.

It is also not known how the various spawners are arrayed at the time of spawning. The quantity of sperm available probably limits the volume through which the eggs are distributed. For the purpose of this discussion we shall use the concentration of ten thousand to one hundred thousand eggs per cubic meter.

In summary, the species involved in this paper extend for one or two thousand miles of coastline in the temperate zone of the Pacific coast of North and South America and into the tropics of South America. The species are apparently subdivided into stocks or subpopulations extending a few hundred miles along the coast within tens of miles of the coastline in South America and within a few hundred miles of the coast in North America. We assume that these stocks form school groups of a few nautical miles extent and these are comprised of schools of tens of meters radius concentrated at 100 schools per nautical square mile. Within the schools in daytime, there are about 15 kilograms of fish per square meter of surface area. The night-time concentration is assumed to be less dense. Also, in the spawning season, the spawning females and their male attendants segregate early in the evening to spawn and fertilize the spawn and reaggregate with the schools before dawn.

Temporal scales of egg production: The early work on spawning frequency (Hunter and Goldberg, 1979; Alheit et al., this volume) indicates that a female of the genus *Engraulis* may spawn a hundred or so batches of eggs in her lifetime. The female may spawn a limited number of times in the first year of life and in later years may spawn 30 times per year. The spawning appears to be intensified seasonally, beginning in the winter months and persisting for some months, depending on the age, size, and condition of the female and the feeding conditions. Hunter (pers. comm.) believes that spawning rate in *Engraulis mordax* is controlled by the amount of fat stored in previous summer and the feeding conditions at the time of spawning. Hunter and Leong (1981) state that 10 to 15 batches could be spawned using the energy in stored fat and that subsequent spawnings would be derived from feeding during the spawning season. Smith and Eppley (1982) found a correlation suggestive of a link between the zooplankton abundance in the preceeding summer and the larva abundance in the spawning season. Hunter (pers. comm.) believes the pattern of atresia or resorption of oocytes prior to spawning matches this viewpoint since atresia is most common in young fish with little stored fat and with older fish late in the season of heaviest spawning.

On the daily time scale, the collective spawning interval extends from about sundown to a couple of hours after midnight with a propensity to spawn within 3 hours of midnight. It appears that individual females spawn in a very short time because the increasing incidence of samples with newly spawned eggs (fraction of samples with newly spawned eggs) and the increasing abundance of newly spawned eggs (newly spawned eggs per sample) with time are nearly parallel. If individual females spawned over an 8 hours period one would expect the incidence of newly spawned eggs to rise rapidly with the change in abundance following many hours later.

These general features appear to be similar for *Engraulis mordax* and *E. ringens*. The life span of the *Sardinops* is much longer but the number of spawnings or the maximum rate of spawning is not known for this genus. However the daily cycle of spawning is similar in *Sardinops caerulea* (Smith,1973).

Changes of spatial scale with time: At the moment of spawning, the *Engraulis* schools are at the scale of tens of meters and the scale of the egg patches of *Sardinops* and *Engraulis* are on the scale of hundreds of meters (Smith,1973; Smith and Hewitt MS) and the yolk sac larvae patches are on the scale of a few thousand meters (Hewitt,1982). In a period of five days after spawning turbulent diffusion has spread the newly spawned eggs, covering at most a few tenths of one percent of the sea surface in the spawning area to covering nearly 70% of the sea surface at hatching time.

There may be different explanations for the greater intensity of *Sardinops* and *Engraulis* egg distribution off Peru as compared to California and the differences between the *Engraulis* in both hemispheres and the *Sardinops* in both hemispheres. To consider these, we must establish some useful categories of causes for differences in the scale and intensity of patches of eggs. One category of difference can be termed "demographic". That is if the age distribution of the females is older the stock will be made up of larger fishes and for the two genera the size distribution of *Sardinops* females will be larger than *Engraulis* females. Another category of difference can be labeled "behavioral". That is if the individual females behave in such a way as to distribute their spawn in smaller, more compact patches this would retard subsequent dispersal rates relative to females which disperse their spawn in larger, more diffuse patches. Another category of difference causing changes in distribution of sample sizes of eggs could be labeled "environmental". That is the subsequent mixing of the spawning products or the pattern of mortality could in time impose a different sample frequency distribution. We shall discuss these categories in more detail.

Demographic factors affecting the number of eggs per sample: The relationships between fish weight and eggs per gram of fish weight are not completely known for *Engraulis mordax, Engraulis ringens, Sardinops caerulea,* and *Sardinops sagax*. For *Engraulis mordax,* the relationship is apparently linear (Picquelle and Hewitt,1982; Alheit et al.,in prep.) for the period 1980 through 1982 for the central subpopulation. Neither *E. mordax* nor *E. ringens* have been examined with regard to age-specific fecundity as distinguished from size-specific fecundity. Even though age and weight are related, the differences between weight at age and the ranges of weights and ages could explain the differences apparent in the linearity of the fecundity with weight. It is not known how this would affect the distribution of eggs in the sea. If the older or larger females were capable of spawning more eggs into a column of water there could be persistent changes in the egg sample distribution. However, it appears that the *Sardinops* places fewer eggs in a column of water even though the female of the genus *Sardinops* is larger than the female of the genus *Engraulis*.

Another demographic feature is age and size at first maturity. Females of genus *Engraulis* appear to begin maturation in the first year of life while the females of the genus *Sardinops* mature somewhat later and at a larger size. Within *Engraulis mordax* females it is characteristic for the "0" group females to begin spawning later in the season and stop sooner than females of the older cohorts. If there were similar maturational features in the genus *Sardinops,* this could lead to both inter-specific and inter-generic differences by some influence on the number of eggs spawned in a column of water according to size. In this case, smaller movements of smaller females would tend to increase the number of eggs per unit surface area. While this would explain the inter-generic differences it is contrary to the interspecific differences in *E. mordax* with an average female weight of 16 grams while *E. ringens* with higher numbers of eggs per unit surface area had female weights in the range of 25 grams.

In summary, it is not clear how demographic features could by themselves explain the differences in eggs per unit surface area. It seems more likely that demographic features would be coupled with behavioral and environmental factors to change the distribution of spawn.

Behavioural factors affecting the number of eggs per sample: On the geographic scale, if the adults of the species aggregate on a specific spawning site this would tend to increase the number of eggs per unit area within the spawning area. It is known that *Sardinops caerulea* migrated to a spawning site hundreds of miles from the feeding zone. To what degree the *Engraulis* species do this is not known but the *Engraulis ringens* spawning zone appears to be much more restricted in distance from shore than that for *Engraulis mordax*. Thus one source to be considered for the differences in the number of eggs per sample is the degree to which the spawners aggregate for spawning. This increases the chance that areas with new spawn would overlap other spawning sites from previous days and thus the number of eggs per unit surface area would be higher. If this were the main cause the order of concentration at spawning time would be *Engraulis ringens*, *Engraulis mordax*, *Sardinops sagax* and *Sardinops caerulea*. This behavioural factor could interact with population demography if the older and larger females were more capable of assembling denser spawning aggregations.

Another behavioral factor could apply at the individual spawning fish scale. For example, if one species, say an *Engraulis* in this case, were to continually turn and circle while spawning and *Sardinops* were to undertake long spawning runs in a straight line, this could affect the initial concentration of eggs and the subsequent dispersal rate. If linear spawning runs were the usual, this would also interact with the demographic factors by faster swimming rates.

Environmental factors affecting the number of eggs per sample: Temperature, turbulence, predation and production are environmental factors affecting the number of eggs per sample. Temperature influences the developmental rate of the eggs (Table 1) and thus influences the probability that the eggs from two different spawning concentrations would be found in a single sample. For example the largest sample of 1300 samples of *Sardinops caerulea* eggs taken between 1951 and 1959 contained two ages of eggs two days apart in age (Smith, 1973). The probability of this kind of event would increase in colder water. The duration of the egg stage at 13 degrees Celsius is about four days for *Sardinops* and *Engraulis* and two days at 18 degrees. This does not appear to be the case for the stocks under investigation. The IMARPE samples are from warmer temperature than the CalCOFI samples.

Table 1

TEMPERATURE AND INCUBATION TIME FOR
ENGRAULIS MORDAX AND *SARDINOPS CAERULEA*
(ZWEIFEL AND LASKER, 1976)

INCUBATION TEMPERATURE	*ENGRAULIS MORDAX*	*SARDINOPS CAERULEA*
11		5.8 days
11.1	4.7 days	
12		4.8
12.5	4.1	
13		3.9
13.8	3.3	
14		3.3
15		2.8
15.2	2.6	
16		2.5
16.6	2.3	
17		2.2
18	2.0	2.0
19		1.8
19.4	1.7	
20		1.6
20.8	1.5	
21		1.4

Turbulent diffusion could have a major effect on the number of eggs per sample. It appears that both *Engraulis* species and *Sardinops* select areas and seasons which minimize turbulent diffusion and offshore transport (Bakun and Parrish, 1982; Husby and Nelson, 1982) off the Pacific coastline of both North and South America. It seems likely that the differences in egg sample numbers could be controlled by the rate of the turbulent diffusion or by a combination of higher initial concentrations of eggs interacting with the lower rate of turbulent diffusion which this would imply.

The effect of predation on the numbers of eggs in each sample would be to change the probability of more than one day's spawning being taken at the same time. It would also be important to know if predation interacted with behavioral features of the predators including cannibals. For example if the predation were merely incidental to feeding on other food particles there would be a proportional drop in all ages of eggs in numbers per unit area. If there were directed predation on the densest concentrations of eggs there would disproportionately higher losses in the earlier ages at the highest concentrations. This could also have an effect on the differences between *Engraulis* and *Sardinops* eggs as the latter are much larger and may be filtered by more predators. The difference in effects would rest on the relative concentrations per unit volume even though the effect would eventually be expressed in numbers of eggs per unit sea surface. The relative visibility of the *Engraulis* and *Sardinops* eggs would be important for visual predators. The differences between the stocks in different hemispheres would also depend on the abundance and effectiveness of the predators found in those waters in the spawning season. Production may influence the numbers of eggs per sample. One way in which food production could control the numbers of eggs per sample is by increasing the frequency of spawning. So far the applications of the SWFC Egg Production Method have found the frequency of spawning off California to be 14.5% in April of 1980, 10.6% in February of 1981, 12,5% in April of 1981, and 12.0% in February of 1982. Off Peru in August-September of 1981, the percent spawning was 16%. This translates to a group average of mature females spawning each 6 days respectively. Spawning at high frequency would influence the chance of two spawning patches overlapping which would increase the range of egg numbers and increase the chances of sampling the origin of an egg patch which would increase the frequency of sampling large numbers of eggs less than the maximum.

Another mechanism for production to influence the number of eggs in a sample is by controlling the feeding behavior of the reproducing stock. For example if the stock were distributed so as not to depress the number of herbivores, the feeding behavior of *Engraulis* and *Sardinops* would be by biting-diminishing the incidence of cannibalism by inadvertant filtering. If production were lower and the growth of the herbivore populations were depressed by the fish, then the incidence of filter feeding and incidental cannibalism would increase, diminishing the numbers of eggs per sample.

Another factor controlled by production would be if the mean motion of that portion of a school which is spawning were reduced in favorable feeding areas and increased in less favorable feeding areas. For example a daytime school may contain 15,000 grams of adult fish per square meter of sea surface area over the school. With no net motion nor spreading of the school at night, there would be 7,500 grams of females and about 1000 grams of spawning females per square meter of sea surface area. With a batch fecundity of 500 eggs per gram, there would be 500,000 eggs per square meter, a number higher than yet observed for any of the four stocks considered here. If the feeding activities carried the school 250 meters during the half-hour spawning period there would be 2000 eggs per square meter. This number is exceeded in about 20% of the samples of *E. ringens*, 3% of the samples of *E. mordax*, 15% of the *S. sagax*, and less than 1% of the samples of *S. caerulea*.

SUMMARY

1) The numbers of eggs of *Engraulis ringens* off Peru per square meter exceed those of *Engraulis mordax* off California.

2) The numbers of eggs of *Sardinops sagax* off Peru per square meter exceed those of *Sardinops caerulea* off California.

3) Both off Peru and California the numbers of eggs from the genus *Engraulis* exceed those of the genus *Sardinops*.

4) A wide variety of demographic, behavioural and environmental factors has been discussed singly and jointly and there needs to be special research conducted to identify the most important influences. It seems plausible that the differences in numbers of eggs per square meter between the genera *Engraulis* and *Sardinops* are caused primarily by demographic differences in the populations and that the differences between the Peruvian stocks and Californian stocks are caused primarily by environmental factors in concert with behaviour.

5) Regardless of the causes of the difference in egg distribution among the four stocks off Peru and California, caution is warranted in establishing the optimum number of samples for calculating the egg mortality using the Southwest Fisheries Center Egg Production Method. It appears that more samples will be needed for a fixed precision in the Peruvian anchoveta compared with the other three stocks.

6) Some of the features distinguishing the four stocks studied here may effect the efficacy of the mortality regression method and its precision. Particularly those features implying selective predation and cannibalism (Santander et al., MS) could strongly affect the assumption of equal variance in real or porportional terms for the regression of egg abundance on time. Also environmental changes in the rate of dispersal of the eggs could also complicate regression methods which require stability of variance among the elements of the regression.

7) The degree of difference among the eggs per unit surface area, when all have likely had an origin in a compact volume for external fertilization, is likely to portend great differences in the biology of the embryonic stages and the ultimate contribution of fluctuations of position and survival during this stage to population control mechanisms.

REFERENCES

Alheit, J., V.H. Alarcon and B.J. Macewicz (in prep.) Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*.

Alheit, J., J.R. Hunter, B. Alegre, V.H. Alarcon and B.J. Macewicz (This volume). Batch fecundity and spawning frequency of various anchovy. (Genus: *Engraulis*) populations from upwelling areas and their use for spawning biomass estimates.

Bakun, R. and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. Calif.Coop.Oceanic Fish.Invest.Rep. 23:101-112.

Fiedler, P.C. 1978. The precision of simulated transect surveys of northern anchovy, *Engraulis mordax*, school groups. U.S. Fishery Bulletin 76:679-685.

Hewitt, R.P. 1982. Spatial pattern and survival of anchovy larvae: Implications of adult reproductive strategy. Doctoral Dissertation University of California at San Diego, Scripps Institution of Oceanography, Marine Biology. 187 p.

Hewitt, R.P., P.E. Smith and J. Brown. 1976. Development and use of sonar mapping for pelagic stock assessment in the California Current area. Fishery Bulletin U.S. 74:281-300.

Hunter, J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fishery Bulletin U.S. 77:641-652.

Hunter, J.R. and C. Kimbrell. 1981. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fishery Bulletin U.S. 78:811-816.

Hunter, J.R. and R. Leong. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin U.S. 79:215-230.

Hunter, J.R. and B.J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax* during the 1979 spawning season. Calif.Coop.Oceanic Fish.Invest.Rep. 21:139-149.

Husby, D.M. and C.S. Nelson. 1982. Turbulence and vertical stability in the California Current. Calif.Coop.Oceanic Fish.Invest.Rep. 23:113-129.

Kramer, D.M., M. Kalin, E. Stevens, J. Thrailkill and J. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech.Rep. NMFS Circ. 370.

Lynn, R.J., K.A. Bliss and L.E. Eber. 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, stability, dynamic height, oxygen and oxygen saturation in the California Current, 1950-1978. Calif.Coop.Oceanic Fish.Invest.Atlas No. 30. 513 p.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. pp. 201-220. *In* Workshop on the effects of environmental variations on the survival of larval pelagic fishes (G.D. Sharp, ed.) IOC/UNESCO, Paris.

____________ (in prep.). Antagonism between population diffusion and density dependent habitat selection: Prediction of anisotropic gene flow.

Picquelle, S.J. and R.P. Hewitt. 1982. The northern anchovy spawning biomass for the 1982-83 California fishing season. Southwest Fisheries Center Admin.Rep. LJ-82-16. 37 p.

Santander, H. and O.S. de Castillo. 1979. El ictioplancton de la costa peruana. Bol.Inst.Mar Peru Callao 4(3):69-112.

Santander, H., J. Alheit y P.E. Smith (in prep.) Estimación de la biomasa desovante de la anchoveta peruana, *Engraulis ringens*, del stock central y norte en 1981 usando el 'Método de Producción de Huevos'. Bol.Inst.Mar Peru Callao. 70 p.

Santander, H., J. Alheit, A.D. MacCall and A. Alamo. (This volume). Egg mortality of the peruvian anchovy (Engraulis ringens) caused by cannibalism and predation by sardines (Sardinops sagax).

Santander, H., P.E. Smith y Alheit. 1982. Determinación del esfuerzo de muestreo requerido para el estimado de producción de huevos de anchoveta, Engraulis ringens, frente al Peru. Bol.Inst.Mar Peru Callao 7(1):1-18.

Smith, P.E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp.P.-v.Réun. CIEM 164.282-292.

Smith, P.E. 1981. Fisheries on coastal pelagic schooling fish. pp. 1-29. In Marine Fish Larvae: Morphology, ecology, and relation to fisheries (R. Lasker, ed.) Washington Sea Grant Program, University of Washington Presse, Seattle and London.

Smith, P.E. and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp.P.-v.Réun. CIEM 173:77-84.

Smith, P.E. and R.W. Eppley. 1982. Primary production and the anchovy population in the southern California bight: Comparison of time series. Limnol. and Oceanogr. 27:1-17.

Smith, P.E. and R.P. Hewitt. (in prep.) Spatial inferences from replicate samples of anchovy eggs.

Smith, P.E. and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish.Tech.Pap. 175:1-100.

Stauffer, G.D. and S.J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Southwest Fisheries Center Admin.Rep. No. LJ-80-90.

Stauffer, G.D. and S.J. Picquelle. (in prep.) Egg production estimates of spawning biomass of the northern anchovy, Engraulis mordax, for 1980 and 1981.

ON THE VARIABILITY OF POPULATION BIOLOGY RATES: EXAMPLES FROM THE CALIFORNIA PELAGIC FISHERIES

(Summary only)

by

R.H. Parrish and D.L. Mallicoate

Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831
Monterey, California 93942
U.S.A.

SUMMARY

Traditional single species fisheries models have recently received a great deal of criticism, and a shift in emphasis to multispecies and ecosystem models has been advocated. An alternative approach is to develop more realistic single species models that overcome the limitations of most present models. Where sufficient information is available this could be accomplished by replacing spawner-recruit relationships with separate model components from eggs, larvae, and juveniles and by increasing the complexity of the post-recruit, or adult components of the model so that egg production rather than spawning biomass is the index of reproduction.

More precise steady state and density-dependent fisheries models are, of course, not likely to be of much more utility than present models. What is needed is assessment or prediction of the potential variability of populations. This could be accomplished through real-time measurement of population rates or through development of predictive models which describe the relationships between population rates and easily measured climatic or biotic factors.

Fishery sampling and resource surveys carried out through the CalCOFI program in California have produced a data base which is approaching the magnitude which will allow the direct assessment of egg production, egg mortality, larval growth and mortality, and post-recruit growth and mortality. The sampling programs and data base on juveniles are much less extensive than those for eggs, larvae, and post-recruits; however, research on juveniles is increasing.

Expansion of the post-recruit and egg production components of fisheries models is possible on stocks which have a time series of traditional fishery sampling. We have used California Department of Fish and Game fishery sampling and sea survey data on anchovy, *Engraulis mordax*, and mackerel, *Scomber japonicus* to describe the variability of post-recruit life history rates, including the following:

- seasonal variation in growth
- regional variation in growth, age composition, and spawning season
- age-dependent variations in spawning season, spawning frequency, annual fecundity and distribution with depth
- interyear variations in growth, age-at-maturity, condition factor, and spawning frequency.

The extreme variability of population rates observed in California pelagic fisheries and the potential accumulative or synergistic effects of combinations of these rates suggest that the population biology of these stocks are exceedingly complex. Significant improvement of single species models would be expected through either real-time measurement of population rates or through the development of environmentally-dependent predictive models of the rates.

ON LONG-TERM CHANGES IN ABIOTIC AND BIOTIC CONDITIONS

by

A.A. Elizarov

All-Union Research Institute of Marine Fisheries
and Oceanography (VNIRO)
17, V. Krasnoselskaya
Moscow, B-140, 107140
USSR

The patterns of long-term changes in the Earth's natural characteristics are among the main subjects of modern oceanological investigations. Results of these investigations affect long-range forecasts of atmostpheric and hydrospheric temperature and of ice conditions, predictions of year-class strength of the most important commercial species and of substantial changes in their distribution.

Needless to say, the biotic phenomena are functionally related to abiotic conditions. The strength of year-classes of commercial species, the annual recruitment to fish populations and their total stocks are closely related to annual and long-term variations in abiotic (physical and chemical) conditions.

In many cases, as in the case of the anomalous development of "El Niño", a close relationship between the ichthyomass fluctuations and the environmental conditions is readily apparent, while in other (most often not extreme) situations it is obscured by some local or short-term processes and phenomena. The latter calls for a close examination of the time of onset and the periodicity of recurrence of extreme years.

For many reasons, such as instability of the processes, inadequate observation series etc., the formal mathematical processing of observation series is as yet unsatisfactory, especially in revealing extreme situations which are of great practical significance.

It has been noted before that there is a very great similarity (pointing to real regularity rather than to randomness) in the onset of extrema in such dissimilar and remote phenomena as: "El Niño"; the intensity of warm water influx to the southern Barents Sea; the dispersion of icebergs by the Labrador Current; the strength of cod year-classes in the fishing areas of the North Atlantic and the Norwegian and Barents Seas; the transport of the West Greenland Current; the air pressure difference between Ponta Delgado and Stikkysholm, etc. (Elizarov, 1974; 1976; 1962).

Without exception, in all these observation series the extrema fall on 1949-1951 (most often 1950), 1956-1958, 1964-1966 and 1970-1972. In the North Atlantic other years with extreme situations have been observed, and the analysis of these suggests the existence of two independent quasi-seven year (mostly six-eight year) rhythms of long-term changes in the water circulation intensity and the year-class strength of important commercial fish species. Recent data are consistent with this conclusion. For example, water temperature minima along the Kola meridian occurred in 1941/42, 1948, 1956, 1963, 1971 and 1979, as well as in 1945/46, 1953, 1958, 1966, 1974 and 1981/(82?), while maxima occurred in 1937/38, 1944, 1950, 1957, 1964, 1970, 1975/76, as well as in 1939, 1947, 1954, 1959/60, 1967/68, 1973 and 1980.

Needless to say, a purely formal approach would lead to the conclusion that the minima and maxima set in on the average practically every 3.5 years over the period of 40 years. However, this formal conclusion in inconsistent with the pattern of the analysed wave. Indeed, the interval between adjacent troughs or peaks varies constantly from 2-3 to 4-5 years. The quasi-seven year rhythms are also indicated by the frequency of "El Niño" recurrence and the rhythms of other biotic and abiotic processes (Elizarov, 1974).

The proposed construction is undoubtedly somewhat artificial, yet based on its regularities a certain warming in the southern Barents Sea in 1983/84 and a cooling and, consequently, deterioration of reproductive conditions for boreal fishes in 1985/86 may be expected. As has been said before, formal mathematical computation is at present hardly applicable for prediction purposes because of the instability of major processes and almost complete ignorance of the mechanisms of long-term fluctuations.

To be sure, our artificial construction is by no means the only possible variant. It would be of interest to recall the main concept and principles of predicting long-term cyclic variations in the intensity of Atlantic water influx to northern seas and the associated (related to water temperature variations along the Kola meridian) fluctuations in cod stocks advanced by G.K. Izhevskij more than twenty years ago (1961). According to this author, the most pronounced waves of warm current intensity in our northern seas are those with periods of 4-5, 8-10 and 18-20 years. The maximum productivity effect is achieved in the case of superposition of all the three waves which were attributed by the author to tidal cycles.

Superposition of wave peaks (nearly complete) in 1949-50 resulted in large stocks of cod in 1954-55. In many cases, for example in 1935 and 1954, there was a superposition of two of the three waves. Numerous new data have been collected since the work of G.K. Izhevskij was published in 1961, and it would seem appropriate to test the validity of his conclusions using recent material.

First let us extend the series forming his 4-5 years wave. The minima of 1921, 1926, 1930, 1939 and 1944 are followed by those of 1949/50, 1954, 1959/60, 1964, 1969/70, 1975 and 1980. There are no substantial changes here, except that it may be more correct to speak of the 5-6 year wave. The next series of 1912, 1921, 1930, 1939 and 1949/50 will be extended to include 1959/60, 1970 and 1980. This is a striking quasi - 10 year cycle which tends to have peaks in the last years of the decades. The 18-20 year cycle years of 1903, 1921 and 1939 are followed by 1957 and 1975, i.e. practically all the intervals between wave peaks are equal to 18. The author in the late 1950's could hardly expect nature to be so punctual.

The data illustrated here indicate that as a result of superposition of the waves there were relatively favourable conditions for the formation of good year-classes in the early and mid-1970's, which is generally consistent with the known facts.

According to G.K. Izhevskij (1961, 1964) there is a fairly good agreement in the times of onset of maxima and minima in physical and biological processes, from where follows the basic possibility of conditional calculation of commercial fish stocks by summation of oceanographic indices for the birth years of year-classes on which the fishery is based.

By itself, the coincidence of the extrema does not on any account point to causal connection between, for example, an increase or a decrease in water temperature and the year-class strength of a certain biological species. Until their causality has been proved, these connections can only be regarded as structural (may be effects of a common cause, etc.).

In the discussion of this problem it seems to be important to draw attention to investigations dealing with detailed consideration of the dependence of early development of fish on environmental factors. It has been found, for example, that the survival of young Arcto-Norwegian cod and, consequently, the biomass and abundance of the year-class recruited to the fishery are dependent on the oceanological conditions during the early three years of life (Baranenkova and Kholina, 1967; Pnomarenko, 1970). This extremely important conclusion permits the use of Izhevskij's formula for calculating stocks from oceanographic indices (1961) with allowance for three years of early development. Below are given arbitrary stock indices for the Arcto-Norwegian cod calculated with the use as an oceanographic index of mean water temperatures along the Kola section. 1959 was chosen because this was the earliest year considered by G.K. Izhevskij.

Table 1.

Year	Stock Index	Year	Stock Index
1959	12.52	1971	10.15
1960	11.87	1972	11.00
1961	11.25	1973	11.50
1962	12.08	1974	11.42
1963	12.32	1975	11.76
1964	12.81	1976	11.99
1965	12.49	1977	12.41
1966	11.55	1978	12.77
1967	11.53	1979	12.50
1968	11.25	1980	12.04
1969	10.68	1981	10.67
1970	10.25	1982	9.50

It is easily seen that the stock index calculated from oceanographic indices is highest in 1964 and lowest in 1982, which is generally in agreement with available data. It would also be noted that in 1982 both the stock and the oceanographic indices are at the lowest level for the entire period of observations of water temperature and catch since 1921.

However, this is not the only interesting thing about the table. One can hardly fail to observe that there is also a certain periodicity in stock fluctuations, the maxima falling on 1959, 1964, 1973 and 1978 and the minima on 1961, 1971 and 1982.

The 4-5 year or the 10-year wave is thus manifested, depending on the contribution to the total value.

It therefore appears that long-term fluctuations in abiotic and biotic conditions follow a certain pattern which permits the onset of one or another extremum to be predicted, at least approximately. Formalization of forecasting on the basis of these regularities has so far been impossible, for there is no way of predicting the real contribution of different periodicity waves to the total value of the characteristics.

REFERENCES

Baranenkova, S.A. and N.S. Kholina. 1967. Chislennost' i drefj ikrinok, lichinok i sravnitel'nye dannye o vyzhivaemosti segoletkov (donnye stadii) pikshi Barentseva morya v 1959-63 gg. (Abundance and drift of eggs and larvae, and comparative data on the survival of the Barents Sea haddock underyearlings (bottom stages) in 1959-63). Tr. PINRO, v.XX, Pishchepromizdat, Moscow.

Elizarov, A.A. 1962. O mezhgodovykh kolebaniyakh intensivnosti Labrador-skogo i Zapadno-Grenlandskogo techenij i vozmozhnost' prognoza temperaturnykh uslovij v promyslovykh rajonakh Severo-Zapada Atlanticheskogo okeana. (On annual variations in the intensity of the Labrador and West Greenland Currents and the possibility of forecasting temperature conditions in the fishing areas of the Northwest Atlantic). Okeanologiya. No.5:796-809.

____________. 1974. O mnogoletnikh kolebaniyakh temperatury vody i promyslovoj produktivnosti v rajonakh Severnoj Atlantiki, Norvezhskogo i Barentseva morej. (On long-term water temperature variations and commercial fish production in the North Atlantic, Norwegian and Barents Sea areas). Tr. VNIRO. v. 98:7-22.

____________. 1976. Dolgoperiodnye svyazi izmeneniya okenologicheskikh faktorov i urovnej bioproduketivnosti arkticheskikh bassejnov (na primere Severo-Zapadnoj Atlantiki). (Long-period relations of variations in oceanological factors and in the levels of bioproductivity of Arctic basins (with reference to the Northwest Atlantic)). Tr. VNIRO. v.112:16-22.

Izhevskij, G.K. 1961. Okeanologicheskie osnovy formirovaniya promyslovoj produktivnosti morej. (Oceanological principles as related to the fishery productivity of the seas). Pishchepromizdat, Moscow. 216 p.

____________. 1964. Sistemnaya osnova prognozirovaniya okeanologicheskikh uslovij i vosproizvodstva promyslovykh ryb. (System analysis as a basis for prediction of oceanological conditions and reproduction of commercial fish). Izd.MGU, Moscow. 165 p.

Pnomarenko, I.Ya. 1970. O vozmozhnosti dolgosrochnogo prognozirovaniya chislennosti promyslovogo stada i proizvoditel'nosti tralovogo promysla treski s terkhletnej zablagovremennost'yu. (On the possibility of long-range forecasting of commercial cod stock abundance and trawl fishery efficiency three years in advance). Materialy rybokhozyajstvennykh issledovanij Severnogo bassejna. No.16(1), Murmansk.

ESTUDIO COMPARATIVO DE LA DINAMICA DE UNA ESPECIE PELAGICA Y OTRA DEMERSAL MEDIANTE UN MODELO DE SIMULACION (sólo Resumen)

Por

J. LLeonart y B. Roel

Instituto de Investigaciones Pesqueras
de Barcelona, Paseo Nacional s/n
Barcelona 3
ESPAÑA

Resumen

Se ha diseñado un modelo de simulación que reproduce las diversas fases de la dinámica de una población de peces en explotación. El modelo se ha aplicado empleando los datos de capturas y parámetros poblacionales disponibles de la anchoveta peruana y la merluza sudafricana. Se han escogido estas dos especies por considerarlas representativas de medio pelágico y demersal respectivamente, y por constituir pesquerías que son o han sido muy importantes, por lo cual la información disponible es abundante. Las estrategias de estas dos especies son claramente distintas, y al hacer la comparación de estas dos poblaciones mediante el modelo de simulación se discuten brevemente estas diferencias.

PRODUCTION MODELS AS APPLIED TO SUB-STOCKS DEPENDING ON UPWELLING FLUCTUATIONS

by

Pierre Fréon

ORSTOM 24
rue Bayard 75000
Paris, France

Resumen

La plataforma continental del oeste de Africa entre los 11°N y 24°N representa un área de pesca muy rica relacionada a afloramiento costero. En esta área se presentan dos poblaciones de sardinas (*Sardinella aurita* y *Sardinella maderensis*), cuyos adultos migran largas distancias dentro del área descrita. La explotación es intensiva y variada, pero debido a lo poco adecuado de las estadísticas de captura no es posible establecer modelos de producción para toda la población de cada especie.

Dos áreas principales de cría reciben importantes sub-stocks de individuos jóvenes, los que permanecen en dichas áreas hasta su primer desove. Una de las áreas de cría, localizada en la "Petite Côte" de Senegal, es explotada intensamente, disponiéndose de series de datos de captura y esfuerzo de pesca (de la pesquería semi-industrial y artesanal).

Se discuten dos hipótesis principales, una relacionada a la estabilidad de la tasa de explotación fuera de "Petite Côte" y la otra, que se relaciona a parte del reclutamiento. Bajo estas dos hipótesis, cada sub-stock correspondiente puede ser considerado separadamente. Los datos colectados sugieren que los rendimientos de la pesca están relacionados con el esfuerzo de pesca local, y con la intensidad del viento responsable del afloramiento costero. La interpretación del efecto del afloramiento sobre los rendimientos se conoce todavía en forma incompleta: hay probablemente una adición a la fertilización del ambiente, y es probable que haya un aumento de la disponibilidad de sardinas asociadas al aumento de la productividad.

Se han establecido diferentes modelos de producción en base a análisis de regresión linear múltiple, incluyendo rendimiento de la pesca, esfuerzo e intensidad de vientos, tales como:

$$\text{c.p.u.e.} = a \exp (a/f) + b\bar{V} + \varepsilon$$

Donde c.p.u.e. es la captura por unidad de esfuerzo para el año (n), f es el esfuerzo de pesca durante el mismo año, V es la intensidad promedio de los vientos durante los años (n) y (n-1), a, b y c son constantes, y ε es el residuo. Las hipótesis preliminares son confirmadas indirectamente y se discuten los resultados obtenidos.

Bajo las condiciones presentes de explotación, el máximo rendimiento sostenible de *Sardinella spp* en la "Petite Côte" debe fluctuar entre 56 000 y 90 000 toneladas métricas por año. La actual tasa de explotación está próxima a su óptimo y se teme que una disminución de la intensidad del afloramiento (por ejemplo causada por la velocidad del viento), y/o un aumento del esfuerzo de pesca pueda afectar seriamente los stocks.

Sin embargo, los datos actuales no permiten una evaluación precisa de la producción para condiciones extremas de intensidad de viento y esfuerzo de pesca mayores que los esfuerzos de pesca en las áreas costeras, a través de varios métodos:

- la extensión de las áreas de pesca que está actualmente limitada por el tipo de embarcación la localización de los lugares de desembarque,
- mantenimiento de un tipo de explotación flexible con la finalidad de poderlos ajustar rápidamente a las fluctuaciones de producción que pueden estar relacionados a la intensidad de los vientos, en relación a este último punto, la dualidad de la pesquería, artesanal y semi-industrial, tiene gran interés.

INTRODUCTION

The West African continental shelf, extended from 11°N to 24°N, represents a rich fishing ground related to coastal upwelling. Two populations of sardines (*Sardinella aurita* and *Sardinella maderensis*) are present, the adults of which migrate over long distances within the mentioned area. Exploitation is intensive and varied, but due to the inadequacy of fishing statistics it is not possible to establish production models for the entire population of each species.

Two principal nurseries receive important "sub-stocks" of young fish which remain present until their first spawning. One of the nurseries, located on the "Petite Côte" of Senegal, is intensively exploited and statistical catches and fishing effort series are available. The study of this nursery is the object of this paper.

SARDINE STOCKS AND SENEGALESE FISHERIES

The biology of the two sardine species has been studied by various authors. These references are available in Boely's synthesis (1980). *Sardinella aurita* constitute a single stock which can be subdivided in three "sub-stocks": two important nurseries are observed, one in Mauritania and the other in Senegal on the Petite Côte (Figure 1). There young fishes remain present until their first spawning and then enter in the common sub-stock of migratory adults which moves over the continental shelf between 11°N and 24°N. These migrations occur over grounds generally deeper than 25 m in relation with the thermal front (Boely et al., 1978). So, adult fishes are available in Senegal only during 5 or 6 months per year, and mainly for long range fishing boats.

Sardinella maderensis nurseries localities are similar to *Sardinella aurita* (Figure 1) but here the young fish migrations are preponderant inside each nursery and generate local variations in availability. Opposed to the case of *Sardinella aurita*, the adult sub-stock has a low numerical importance, at least in Senegal, and it seems that exchanges between the two nurseries, if existing, are insignificant.

Senegalese fisheries are subdivided in two types: semi-industrial and artisanal. The first one is made up of a 25 m overall mean length, purse-seines fleet, already described in detail (Champagnat, 1966; Boely and Chabanne, 1975), for which the number of units has fluctuated between 10 and 20 during the last 15 years. The second one is characterized by the use of wooden canoes. This type is more diversified as it uses surrounding gill-nets, small purse-seines and beach-seines (Freon et al., 1979). The Senegalese fishery is exclusively a coastal activity. It is developed on Petite Côte where mainly young fishes are captured (Figure 2).

BASIC HYPOTHESIS

For *Sardinella aurita* the recruitment of young fishes in Senegal has two origins. First the main spawning of adults during the period of May and June on Petite Côte, and on the other hand, the secondary spawning of the young fishes themselves at the same locality during October and November before they leave their nursery (Conand, 1977). Although the relative importance of each spawning season has been calculated in terms of larval density, importance in terms of recruitment is still ignored due to the differences in larval and fry mortality between the two cohorts.

Anyway, it is clear that the exploitation of *Sardinella aurita* outside Petite Côte (adult sub-stock or Mauritanian nursery) could have consequences on its abundance only through a stock-recruitment relationship, namely the relation between adult sub-stock and the Petite Côte recruitment. The type of relationship is unknown and its precise knowledge is important from a theoretical point of view in order to forecast Petite Côte sub-stock reactions under strong abundance fluctuations of adults sub-stock.

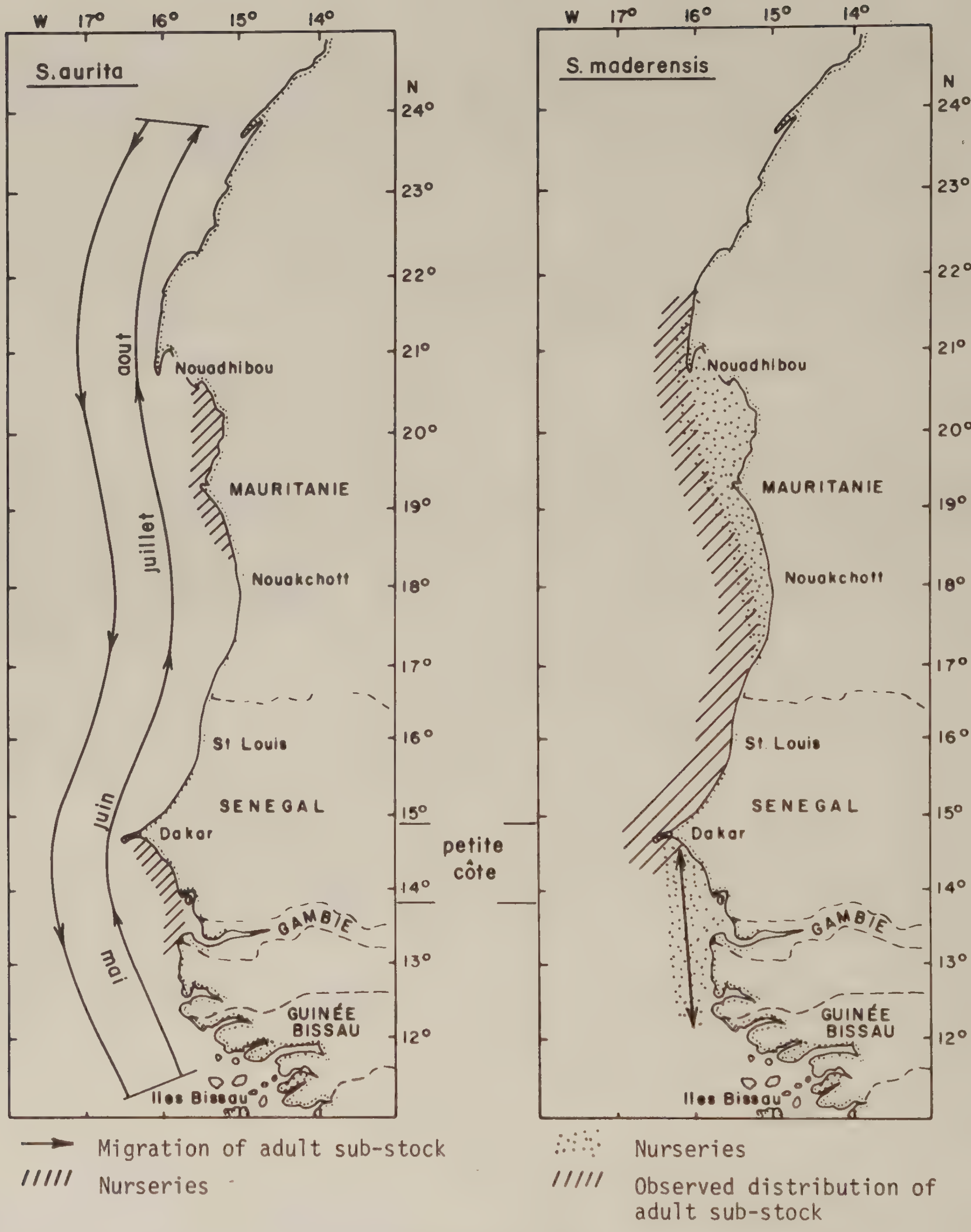

S. aurita
W 17° 16° 15° 14°
N
24°
23°
22°
21°
20°
19°
18°
17°
16°
15°
14°
13°
12°
aout
juillet
juin
mai
Nouadhibou
MAURITANIE
Nouakchott
St Louis
SENEGAL
Dakar
GAMBIE
GUINÉE BISSAU
Iles Bissau
petite côte
S. maderensis
Migration of adult sub-stock
///// Nurseries
Nurseries
///// Observed distribution of adult sub-stock

Fig. 1. *Sardinella aurita* and *Sardinella maderensis* distribution (mai = May; juin = June; juillet = July; aout = August), from Boely et al. (1978).

Harris' analysis (1975) has shown that both density-dependent and stock-dependent processes are needed to establish the basically dome-shaped curve, which appears to be characteristic of the stock-recruitment relationship within the fishes. Now, in the case of adult *Sardinella aurita*, it immigrates and does not stay on the spawning grounds, which could limit the stock-dependent mechanism mainly based on cannibalism. In practice, with any figure retained, it can be considered that the adult sub-stock abundance varies around a mean level. However, the variability of recruitment in the Petite Côte sub-stock related to this former sub-stock is not important, comparatively to variability due to other factors, particularly environmental ones. Indeed, abundance fluctuations in the adult sub-stock has been estimated through one index, i.e., catches per unit of effort (CPUE), of fish larger than 25 cm (Freon *et al*., 1979). During the observed period, annual variations were of one order of magnitude, except for 1975 where the index was strongly under-estimated on account of the target-species change. Curves obtained from other pelagic species (Cushing, 1978) show important variations in recruitment only from three to four orders of magnitude in stock abundance variations, over a critical level of stock size.

So, we have retained as a basic hypothesis that during the period studied, fishing outside Petite Côte did not have any impact on the abundance inside the Petite Côte nursery (Freon *et al*., 1979).

For *Sardinella maderensis* the situation is much more simple since recruitment on Petite Côte seems to be from spawnings by young fish only. In fact the latter leave the nursery from 24 cm of fork-length (probably 1.5 years old) and adults are found in abundance only in Mauritania and north of Senegal. So recruitment on Petite Côte is probably not related to their spawning.

Under this hypothesis it can be considered that CPUE in Petite Côte nursery depends essentially on local fishing effort and eventually on environmental conditions influencing on recruitment, young fishes growth and/or mortality.

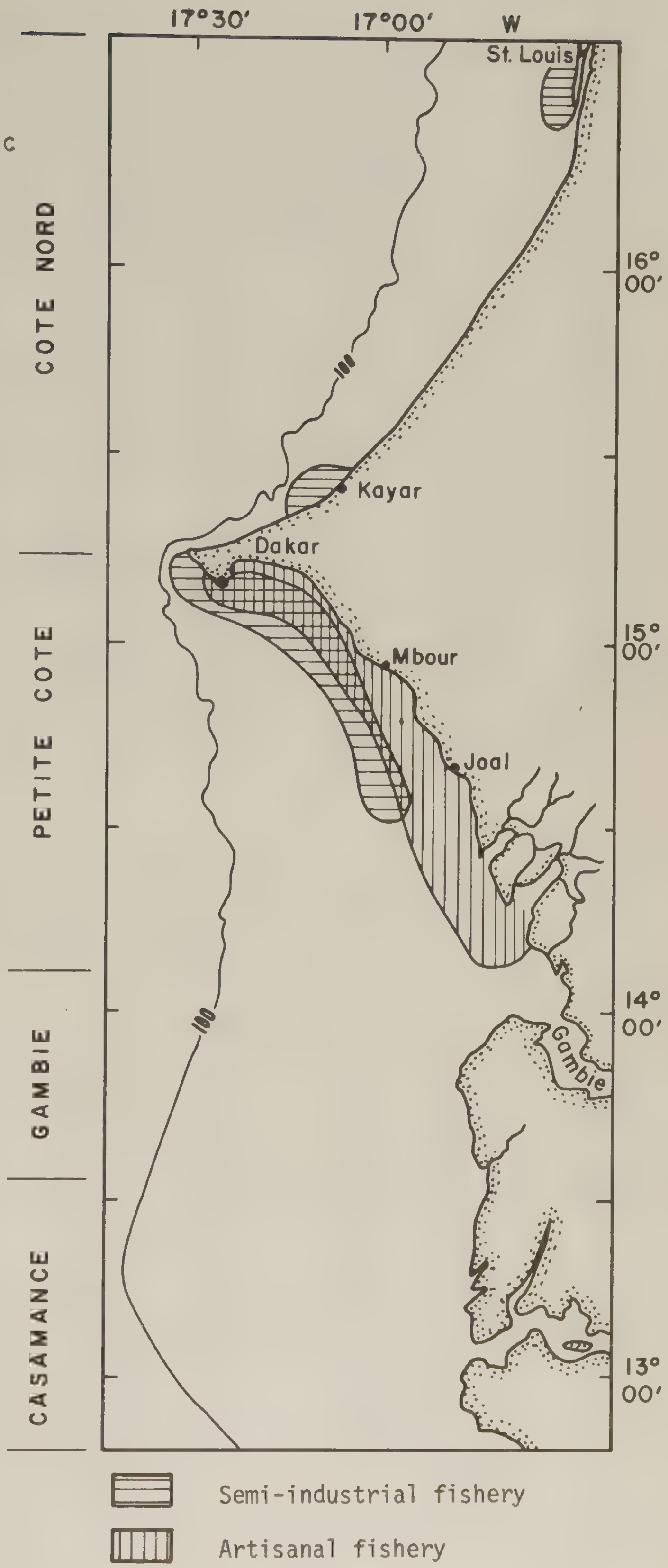


Fig. 2. Senegalese fisheries localization

Table 1: *Sardinella aurita*; catches (metric tons), fishing effort (10 hours' fishing of a standard semi-industrial purse-seiner), and catch per unit of effort (c.p.u.e.) of fisheries in the Petite Côte. Mean wind speed ($\bar{V}$) during the trade wind season of years n and n-1 (m/s).

Years	Indust. Catches	Indust. C.P.U.E.	Indust. Efforts	Artis. Catches	Artis. Efforts	Total Catches	Total Efforts	Total C.P.U.E.	Wind Speed $\left(\frac{2V_n+V_{n-1}}{3}\right)$
1966	4 250	13,54	314	3 970*	293*	8 220	607	13,54	4,93
1967	4 240	11,62	365	3 580*	308*	7 820	673	11,62	4,74
1968	7 060	12,70	556	4 110*	324*	11 180	880	12,70	4,53
1969	9 700	9,86	984	3 360*	341*	13 060	1 325	9,86	4,40
1970	8 390	7,56	1 110	2 710*	359*	11 100	1 469	7,56	4,32
1971	9 440	10,68	884	4 037*	378*	13 480	1 262	10,68	4,70
1972	17 250	16,32	1 057	6 500	398	23 750	1 455	16,32	5,63
1973	17 590	11,38	1 546	11 880*	1 044*	29 470	2 590	11,38	5,53
1974	17 790	9,78	1 819	16 530*	1 690*	34 320	3 509	9,78	5,76
1975	12 430	7,22	1 722	16 900*	2 337*	29 330	4 059	7,22	5,66
1976	14 800	8,06	1 836	24 050*	2 984*	38 850	4 820	8,06	5,79
1977	13 150	8,61	1 527	31 280	3 630	44 430	5 157	8,61	5,72
1978	12 660	9,15	1 384	32 280	3 356	44 940	4 740	9,48	5,21
1979	13 600	6,68	2 035	26 340	4 577	39 940	6 612	6,04	4,68
1980	14 860	7,01	2 120	28 620	3 837	43 480	5 957	7,29	4,98

* Partially estimated data

Table 2: *Sardinella spp.*; catches (metric tons), fishing effort (10 hours' fishing of a standard semi-industrial purse-seiner), and catch per unit of effort (c.p.u.e.) of fisheries in the Petite Côte.

Years	Indust. Catches	Indust. C.P.U.E.	Indust. Efforts	Artis. Catches	Artis. Efforts	Total Catches	Total Efforts	Total C.P.U.E.
1966	6 450	20,3	318	22 840*	1 125*	29 290	1 443	20,3
1967	5 410	17,7	306	20 960*	1 184*	26 370	1 490	17,7
1968	8 860	15,8	561	19 690*	1 246*	28 550	1 808	15,8
1969	14 480	14,3	1 012	18 760*	1 312*	33 240	2 324	14,3
1970	12 640	11,3	1 117	15 610*	1 381*	28 250	2 498	11,3
1971	11 480	13,2	870	19 190*	1 454*	30 670	2 324	13,2
1972	21 720	20,9	1 039	32 000	1 531	53 720	2 570	20,9
1973	26 200	16,3	1 608	33 740*	2 070*	59 940	3 678	16,3
1974	27 770	15,9	1 747	41 480*	2 609*	69 250	4 356	15,9
1975	21 930	12,5	1 754	39 360*	3 149*	61 290	4 903	12,5
1976	26 730	14,7	1 818	54 210*	3 688*	80 940	5 506	14,7
1977	22 400	14,8	1 513	55 200	4 227	77 600	5 740	13,5
1978	17 970	12,7	1 415	58 430	3 767	76 400	5 182	14,7
1979	22 310	10,7	2 085	47 160	4 415	69 470	6 500	10,7
1980	23 800	11,7	2 034	46 440	4 319	70 240	6 353	11,1

* Partially estimated data

AVAILABLE DATA

Detailed data on semi-industrial fisheries have been available since the beginning of exploitation (1961), but catches per unit of effort have been representative of abundance only since 1966. The previous period is considered as experimental (Boely and Chabanne, 1975). Fishing time (total time outside of port minus travelling time) was used as unit of effort (Freon, 1980). Considering the small size of the fishing area and the stability of the exploitation scheme, stratification by zone was not used. In return, unweighted mean of monthly CPUE was computed to get an annual index of abundance.

Artisanal fisheries data is much more incomplete for this very old activity. The first observations were done in 1972, then interrupted from 1973 to 1976 and again have been available since 1977. Estimations were obtained under the hypothesis supposing that semi-industrial CPUE fluctuations are representative of the artisanal ones. This hypothesis is based on similarity of fish length composition of the catches in both fisheries. This is confirmed by the analysis of the available data during the last years.

However, when realized for *Sardinella maderensis* the estimations lead to a global data table where the proportion of estimated catches and efforts is very high, specially before 1972 due to the predominance of gill-nets over artisanal purse-seine. Moreover, this species is not as sought after as *Sardinella aurita* by semi-industrial purse-seiners and consequently the derived abundance index can be biased by target-species changes. For this reason only two data sets were considered: one concerning *Sardinella aurita* and the other regrouping the two species of *Sardinella* and named now: *Sardinella spp.* (Tables 1 and 2). The latter presents the advantage of minimizing target-species change without differing too much from the basic hypothesis relative to production models because the two species have the same biotope.

Anyway, usual reserves must be done about the representativity of CPUE as abundance index, specially on an eventual change of the catchability coefficient related to abundance (Ulltang, 1976; Freon, 1980; Saville, 1980).

MODELLING SARDINE PRODUCTION

Apparent relations between CPUE, fishing effort, and wind intensity

The figure obtained from the 1966-1980 data for *Sardinella aurita* and *Sardinella spp.* show a negative correlation between CPUE and fishing effort, but the adjustment is very poor when applied to the whole period. In return, when data is subdivided in two periods, separated by January 1st, two decreasing lines (or curves) of regression clearly appear (Figures 3 and 4). This suggests the influence of a second factor on CPUE which strongly changed in 1972.

Both sardine species belong to the first level of the trophic web because they eat phytoplankton during their first stages of life and afterwards they will consume zooplankton. On Petite Côte, eutrophication is assumed by a coastal upwelling (Rossignol, 1973) which is probably responsible for the variations in primary production as shown by various authors, of whom Sedykh et al. (1978) in Mauritania. A time plot during the trade winds season (November to May) shows low values of mean wind intensity (expressed in speed) from 1966 to 1971 and high values thereafter, with an exception in 1979 (Figure 5).

On account of an autocorrelation observed in the seasonal wind speed with one year lag (r=8.57) it is difficult to know if the abundance in one year is related only to wind speed during the same year or also during the previous year. The latter case can be supposed because most of the fish caught are between 1 and 1.5 years old. We will see that statistical analysis is of little utility for solving this problem with the available data.

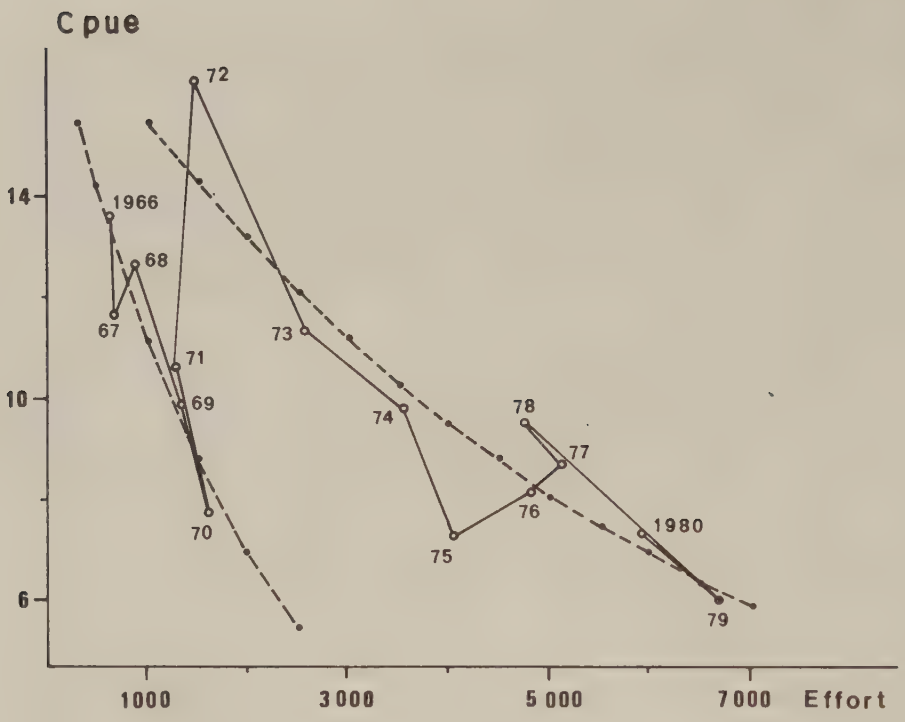


Fig. 3. *Sardinella aurita*; apparent relationship between fishing effort and catches per unit of effort (c.p.u.e.) in the Petite Côte from 1966 to 1980.

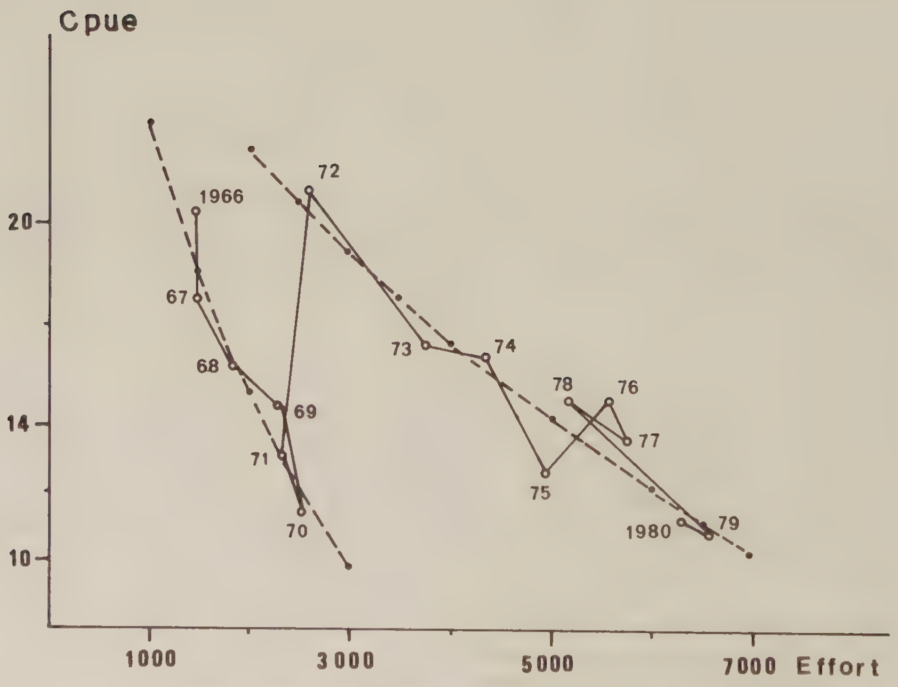


Fig. 4. *Sardinella spp.*; apparent relationship between fishing effort and catches per unit of effort (c.p.u.e.) in the Petite Côte from 1966 to 1980.

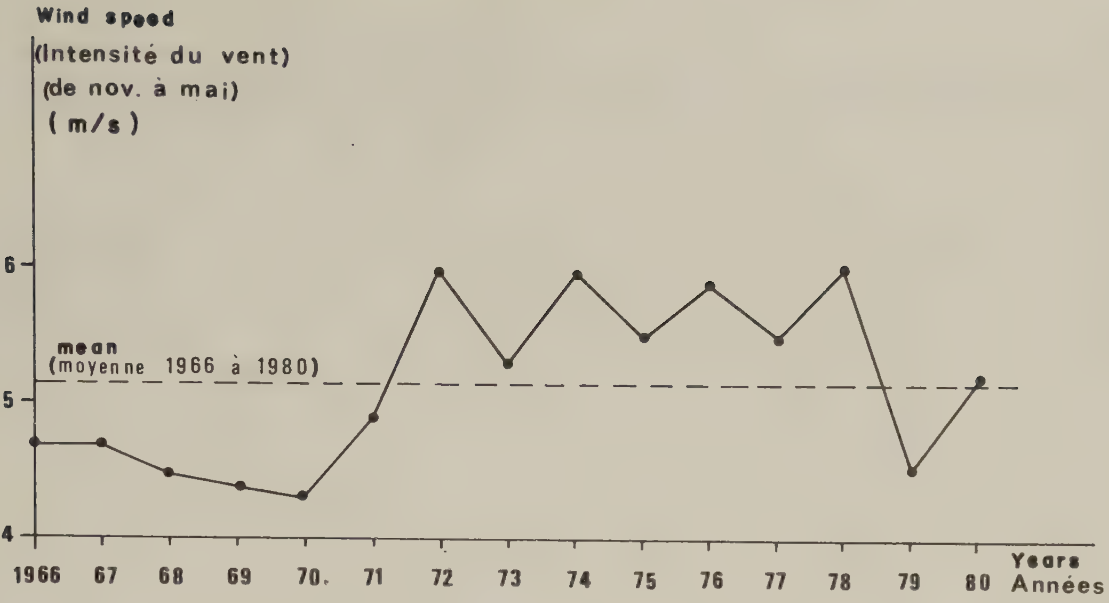


Fig. 5. Time plot of trade wind intensity (from November of year n-1 to May of year n) from 1966 to 1980.

Modelling

Let us suppose that mean CPUE observed during one year would be dependant, first, on fishing effort during the same year, second on mean wind intensity during the trade wind season of the same year and of the previous one. Various multiple-regressions between the three variables were tried, based on different hypothesis about the possible relationship between each variable.

The linear relation between CPUE and effort (Schaefer, 1957) was not used because it supposes that over a certain limit of effort, the CPUE can reach zero, which is in contradiction with our hypothesis for *Sardinella aurita* which states that part of the recruitment is independant of the exploitation on Petite Côte. So, this model seems too pessimistic and we have retained the negative exponential model (Fox, 1970), where the increase of effort assures a more progressive decline in yields. Supposing a linear relation (discussed later) between wind intensity and yield, we combined the following equations:

$$\log \text{CPUE} = -a1\ f + b1 + r1 \qquad (1)$$

$$\text{CPUE} = a2\ \bar{V} + b2 + r2 \qquad (2)$$

where CPUE is the catch per unit of effort during the year n; f is the fishing effort during the same year; $\bar{V}$ is the mean speed of trade winds (various combinations between season of year n and n-1 were used); a, b, c are parameters obtained by adjustment, and r is the residual. From (1) and (2) we obtain:

$$\text{CPUE} = a\ \text{EXP-}a^{-} f + b\ \bar{V} + c + r \qquad (3)$$

Fitting the observed values to the theoretical curve must be done by iterative computation. The data was processed first with a hand calculator using a multiple linear regression, with EXP-a^{-}f considered as a variable, and searching the value of a^{-} which minimizes the multi-coefficient of correlation. Then the data was processed on a desk computer using Marquardt's algorithms (1963). In both cases the results showed that introduction of year n-1 wind speed did not improve very much the fit for *Sardinella aurita*, but was of some interest when used for *Sardinella spp.* model. The best fit was obtained with the following weighted mean:

$$\bar{V} = (2\ Vn + Vn\text{-}1)\ /\ 3 \qquad (4)$$

Anyway, this does not mean that equation (4) represents the real influence of wind on production. In the same way, iterative computations show that fit does not change very much according to a^{-}. However, this parameter value is strongly related to the curve shape over the observed effort values. The optimal value of a^- from a statistical point of view has no biological meaning. This is so when applied to relationship (derived from equation (3)) between catches (C), fishing effort and wind speed, it provides a figure where catches lead to infinite when effort increase under a constant wind speed:

$$C = (a \ \mathrm{EXP}\text{-}a^- f + b \ \bar{V} + c) \ f + r^- \qquad (5)$$

Being one of the main problems of generalized production models, the non-independence between the two variables CPUE and effort (Sissenwine, 1978; Roff and Fairbairn, 1980), we have applied equation (5) for data fitting, using the non-linear regression analysis. This presents the advantage of allowing computation of the parameters confidence limits. None was significant, even with a 90% confidence interval, on account of, first the high number of parameters (4) in comparison with the low number or observations (15). Second, the uncertainty about the a^- value previously mentioned. Nevertheless, it is satisfactory to note that when a^- is fixed at its optimal value in equation (5), the non-linear regression provides for the three remaining parameters (a, b, and c) values which are significantly different from zero using the 95% confident intervals. This means that fishing effort and wind speed statistically have an influence on catches, although the shape of the curve is uncertain over observed effort values.

The problem with the a^- parameter shows that the best statistical fit is not necessarily the most suitable and that the choice of parameters values must also consider the basic hypothesis especially when the stock has not already suffered over-fishing (this problem can be compared with the choice of parameter m in Fox's generalized production model (1975)).

Table 3: Parameters values and confidence intervals got from various regressions on *Sardinella aurita* and *Sardinella spp.* data (tables 1 and 2).

SARDINELLA AURITA

Regression type and equation	Par.	Value	Lower limit	Upper limit	% confid.
LINEAR $cpue = a \ \mathrm{EXP}\text{-}a^- f + bV + c + r$ (1)	a	14.60	9.00 *	20.2 *	95 %
	a^-	.00013 B	-	-	-
	b	2.49	.609	4.37	95 %
	c	-12.89	-24.85 *	-.935*	95 %
NONLINEAR $C = (a \ \mathrm{EXP}\text{-}a^- f + bV + c) \ f + r^-$	a	11.75	5.31	18.21	95 %
	a^-	.00013 B	-	-	-
	b	.911	-.534	2.36	95 %
	c	-2.946	-10.14	4.254	95 %
NONLINEAR $C = (a \ \mathrm{EXP}\text{-}a^- f + bV + c) \ f + r$	a	9.42	2.23	16.61	90 %
	a^-	.00024 M	-.0007	.0011	90 %
	b	1.16	-1.11	3.44	90 %
	c	-1.01	-8.10	6.00	90 %

SARDINELLA SPP.

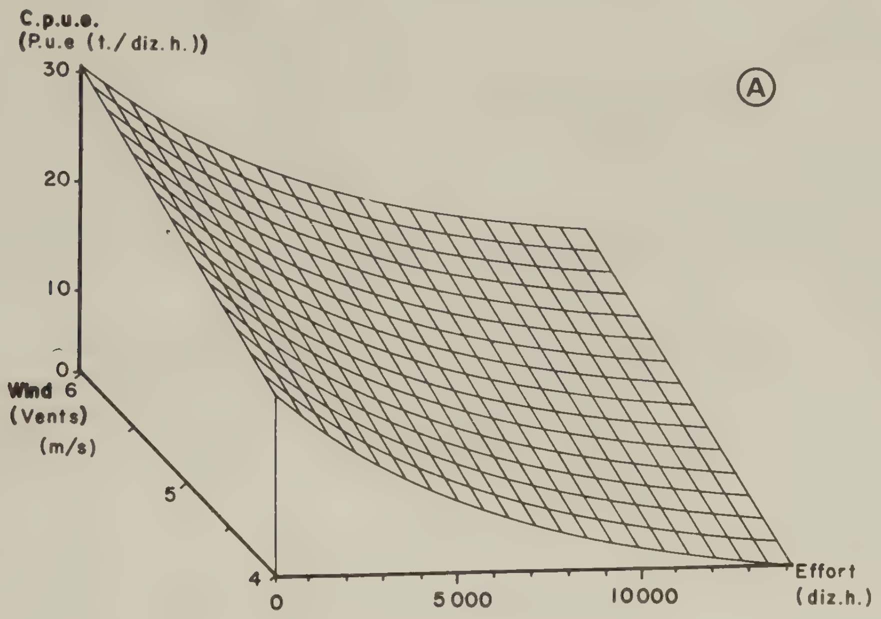
Regression type and equation	Par.	Value	Lower limit	Upper limit	% confid.
LINEAR $cpue = a \ \mathrm{EXP}\text{-}a^- f + bV + c + r$ (1)	a	23.55	16.70	30.40	90 %
	a^-	.00010 B	-	-	-
	b	4.13	2.55 *	5.72 *	90 %
	c	-22.63	-33.91 *	-11.36 *	90 %
NONLINEAR $C = (a \ \mathrm{EXP}\text{-}a^- f + bV + c) \ f + r$	a	14.63	2.58	26.67	90 %
	a^-	.00035 M	-.0004	.0001	90 %
	b	3.230	1.428	5.033	90 %
	c	-6.271	-13.88	1.342	90 %
NONLINEAR $C = (a \ \mathrm{EXP}\text{-}a^- f + bV + dW + c) \ f + r$	a	19.86	10.51	29.21	95 %
	a^-	.00010 B	-	-	-
	b	3.84	.849	6.83	95 %
	c	-12.44	-22.79	-2.098	95 %
	d	-1.646	-5.597	2.306	95 %

B: Optimal biological value of a^- (fixed before computation)
M: Optimal statistical value of a^- (determined by the regression)
W: Wind speed during the summer (from June to October)
*: No strictly valid limits (due to the correlation between cpue and f)

(1): Presented results on the figures

Arbitrarily, we considered as best value for a¯ one which provided a stabilization of catches when the effort increases, inside a realistic interval, and when wind speed is high and stable (Table 3).

Equations (3) and (5) lead to tridimensional figures (Figure 6). We also present two dimensional figures, easier to use, from which four curves have been drawn corresponding to characteristic wind speeds: 4.55 and 5.55 m/s which are the two means of the respective two observed periods (1966-1971 and 1972-1980), 4.0 and 6.0 the extreme mean speed which have been observed since 1951 (Figure 7). Time-plots of observed and computed values have also been presented (Figures 8 and 9).



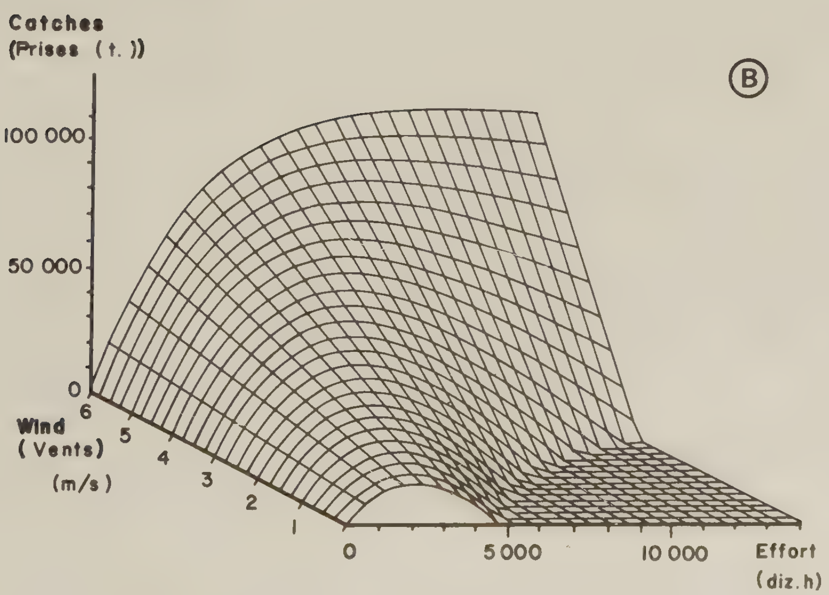


Fig. 6. Tridimensional graphics of the relationship between fishing effort, wind speed and catch per unit of effort (c.p.u.e.) in figure 6A or total catches (C)in figure 6B of *Sardinella aurita* on the Petite Côte. *Sardinella spp.* figures present the same shape and are not included in this paper.

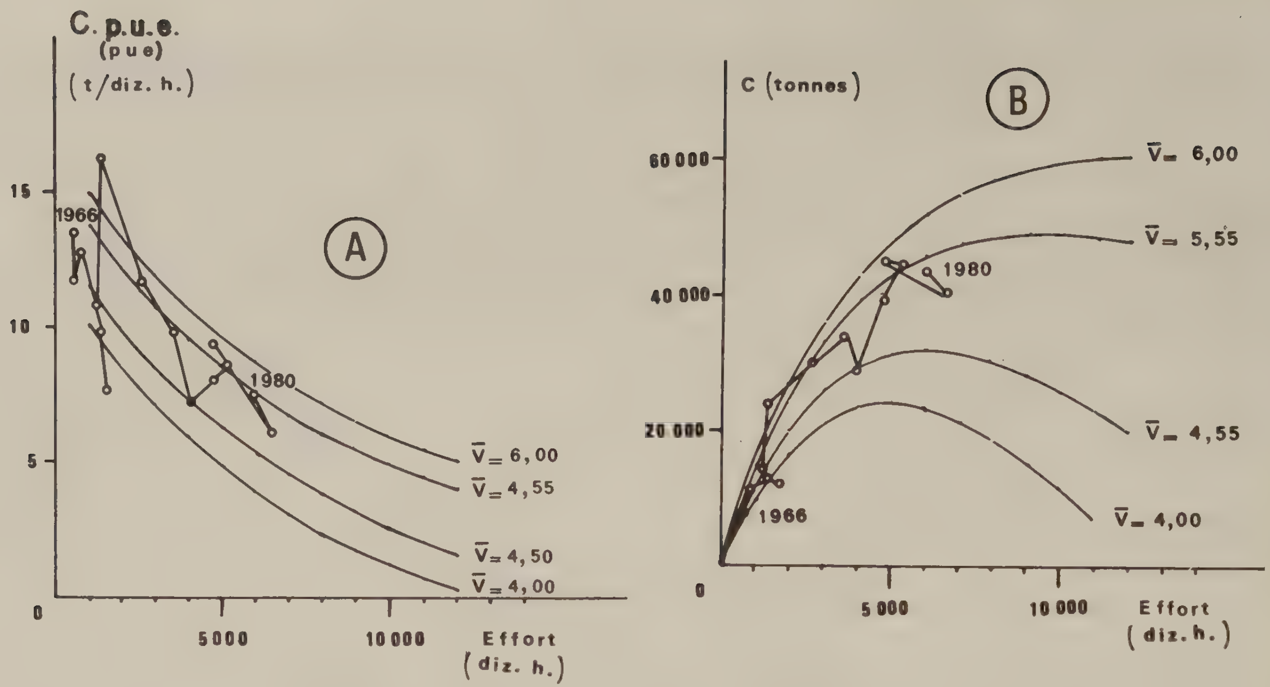


Fig. 7. Two dimentional graphics of the relationship between fishing effort, selected wind speeds and catch per unit of effort (c.p.u.e. in figure 7A) or total catches (C in figure 7B) of *Sardinella aurita* on the Petite Côte. *Sardinella spp.* figures present the same shape and are not included in this paper.

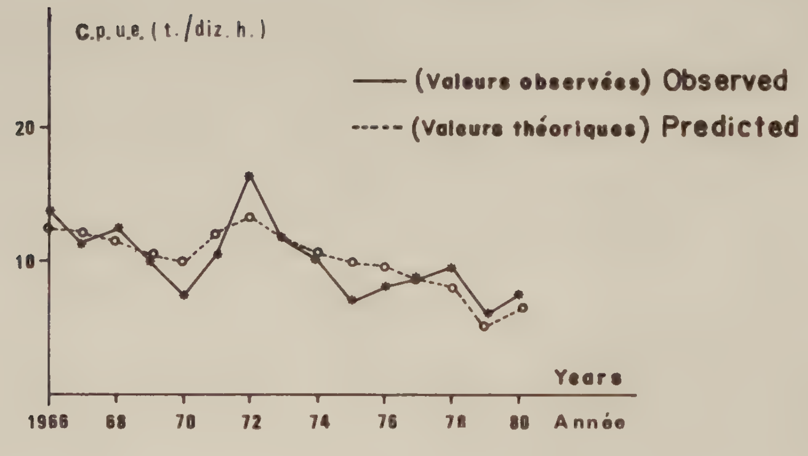


Fig. 8. *Sardinella aurita*: comparison between observed and predicted values of catch per unit of effort (c.p.u.e.) on the Petite Côte.

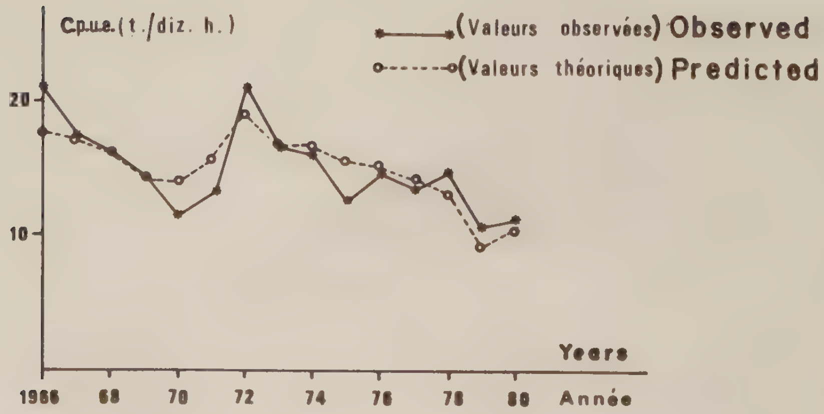


Fig. 9. *Sardinella spp.*: comparison between observed and predicted values of catch per unit of effort (c.p.u.e.) on the Petite Côte.

INTERPRETATION OF THE RESULTS

The considered parameters provide a satisfactory fit for the observed points as a whole to the theoretical curve. Anyway, for some years the residuals have not been negligible for both models (although they never exceded two standard deviations). Two main reasons could explain this fact. First, the precision of data, partially estimated is probably not very good and therefore responsible for a certain amount of the observed variability. Second, obviously fishing effort and wind speed are not the only factors influencing CPUE, and some part of the residual variance comes from numerous other variables.

Among these reasons, some could be in contradiction with our basic hypothesis (relation between adult sub-stock; immigration from other sub-stocks, etc...). These will be further analysed. Other sources of variation could take place at the level of recruitment fluctuations, independently of eutrophication and of parental stock. Thus, recent works (IOC No. 28) suggest that the superficial wind-related turbulence could cause a negative effect on larval survival. We added in the models the mean wind speed during the period following the main spawning (June to October). This improved slightly the fit for the *Sardinella spp.* model showing a negative corresponding regression coefficient (Table 3), but its value was not significantly different from zero even using a 90% confidence interval when calculated with the previously presented method. However, this result is notable because this relationship could be minimized by the positive correlation between the wind speeds during the two described periods of the year.

In the same way, it is evidence that the wind has a negative instantaneous influence on capturability related to school detection and working with purse-seines on rough seas. However, it seems that the favourable effect is dominant here, at least on CPUE expressed in catch per effective fishing time. Last of all, in order to close this non exhaustive list of additional factors, we looked at the influence of other species, considering the multi-specific aspect of the fisheries. This allows predator-prey relationships, but above all in our case, target-species changes related to the relative abundance and to market conditions are also allowed (Boely and Chabanne, 1975). In fact, a study was done (Freon, in press) which shows that during the last years the fishermen balanced their fishing activities in response to the sardine abundance fluctuations by searching for secondary species.

TESTING THE BASIC HYPOTHESIS AND MODEL REVIEW

Testing the hypothesis on the Petite Côte sub-stock independance

Comparison of the fishing effort variations on Petite Côte with the effort on the whole area of the stock distribution indicates a lack of correlation which provides an insurance against a possible confusion between the two variable effects. Moreover, it appears clearly that during the period studied the important fluctuations observed in CPUE on Petite Côte are not explained by changes of the fishing effort within the whole area. The best CPUE obtained by semi-industrial purse-seiners on Petite Côte occurred at the same time with maximum fishing effort on the whole area.

In more details, in the south of Senegal (Casamance, neighbouring Petite Côte), fishing effort was insignificant from 1973 to 1976. From 1977 to 1980 Polish pelagic trawlers got licences and caught up to 70,000 metric tons per year without any sensible effect on yields from the Petite Côte.

These observations do not mean that independance of recruitment in regard to the adult sub-stock will remain true in the future. It is evident that above a certain level of exploitation on the whole stock, the spawners biomass would be too small to assume equilibrium and a collapse could happen unexpectedly, as observed in other small pelagic stocks (Saville, 1980).

Based on the biological references concerning *Sardinella aurita*, two opposed and extreme theoretical cases could be considered. Obviously, the adult sub-stock abundance depends, on a short-termed basis, on its exploitation in the whole area, and on mean-terms on the exploitation of the two nursery sub-stocks which provide its recruitment. The same reasoning can be applied to the Petite Côte recruitment if its main contents would be provided by the adult sub-stock, particularly if the stock-recruitment relationship would be dome-shaped. Under these conditions our model would require stabile fishing effort and absence of over-fishing outside of the described Petite Côte area. This would provide a relatively stable recruitment (having a stable wind intensity) and an important resistance to local over-fishing in Petite Côte.

The second theoretical case supposes that the spawning of the young spawners in the Petite Côte nursery would assume the greatest part of the nursery recruitment. Although not being very realistic, this hypothesis would allow us to consider this stock fraction as completely independant from the other ones regarding its abundance. The situation would be similar to a single stock with a short-life species affording infinite mortality (total emigration) during the second year of life. Under these conditions the sub-stock would be very dependant on fishing effort on Petite Côte, also because an important proportion of the catches are supported by immature fishes. This case would probably justify the use of a linear regression between CPUE and fishing effort, whereas in the former case, a negative exponential regression corresponding to a low production sensitiveness to fishing effort (type m=8.5 in the Fox's generalized production model (1975)) would be suitable.

Reality is probably within these two extremes, since a quasi-constant recruitment is observed all year long on Petite Côte. This fact lets us suppose that adult and young fish spawning provide significant recruitment. Finally, *Sardinella aurita* stock, thanks to its three components distributed in different countries, probably presents a certain resistance to local over-fishing, and complex regulation mechanisms must exist. So the established model for this species seems tolerant enough in regard to the basic hypothesis concerning the stability of the exploitation rate around Petite Côte. However, the stock never supported heavy exploitation on its three sub-stocks at the same time due to the random distribution of fishing licences between coastal and foreign countries. If this situation should occur then our present knowledge would not allow a forecast of yield. Nevertheless, a collapse must be feared.

Sardinella maderensis sub-stock of Petite Côte (which was not studied individually) presents distinct characteristics since we are almost sure that the adult sub-stock does not spawn in this nursery. Associating both species of sardine in a single production model allows us to be more independent of the main basic hypothesis. In return the *Sardinella maderensis* sub-stock offers more sensitivity to local over-fishing.

It should be pointed out that for both species the coastal Petite Côte area is not the perfect nursery where all sardines from the Senegalese region are growing. There are obviously some exchanges of young fishes with the adjacent areas.

Testing hypothesis concerning the wind intensity effect on production

It is essentially the important increase of CPUE between 1970 and 1972 which lead me to include the wind speed variable in the production models. It could be supposed that this increment represents no more than the natural variability expression, independently from the upwelling, or also that the increase originated from a data bias as a change of fishing power. This last event was tested, computing separately the annual CPUE of three vessels which have been working since the early years, always with the same kind of equipment. The figures obtained from these three boats are very similar and correspond exactly to the global data figure. Moreover, it is important to notice that during the year 1972 other anomalies occurred in various eastern Atlantic areas. *Sardina pilchardus* concentrations appearance in Mauritania (Sedykh et al., 1978; Freon and Stequert, 1979), a demographic bloom of *Sardinella aurita* occurred both in the Ivory Coast and in Ghana followed up by a *Balistes carolinensis* bloom (ORSTOM, 1976; FAO, 1980).

The data suggest a linear relationship between CPUE and wind speed. However, various fitting trials with other types of relationships (logarithmic, square, etc...) provide very similar results and it is not obvious that outside the observed range of variation the relation should remain linear. This forces one to use carefully forecasts for extreme wind speed (greater than 6 m/s or lower than 4.5 m/s).

Furthermore, it could be considered that the explicative variable is not the wind intensity and the corresponding upwelling but another correlated factor, i.e., surface temperature. Similar models to those presented were tried, replacing wind speed by surface temperature. They provided analogous results. The fundamental question is now to know if CPUE increase was provided only by the environmentally induced fertilization or also by a certain increase of the sardine availability. The statistical analyses, although difficult to interpret, showed the apparent predominance of the wind speed during the year n (comparatively to year n-1) on CPUE. This suggests a direct influence of wind on sardine availability. Even though, an indirect lag action remains possible because, first, the year n season of trade winds is considered between November of year n-1 and May of year n, second the fish caught is often less than one year old. Rebert (1979) studied monthly variations of sardine productivity in relation with wind anomalies and did not find small scale relations. Anyway the possibility of a combined action of the wind speed (on productivity and on availability) at the year scale is not easy to eliminate. In such a case the expression "production model" should be replaced by "CPUE model" or "catch model".

APPLICATIONS TO SUB-STOCK MANAGEMENT

The previous analysis attempted to prove that the maximum sustainable catch (which is perhaps not exactly comparable to a maximum sustainable yield, MSY) depends on wind intensity. For $\bar{V}$ variations between 4.50 and 5.55 m/s we get the following maximum catches:

Sardinella aurita:	31,000 to 49,000 metric tons
Sardinella spp:	56,000 to 90,000 metric tons

Anyway, it must be pointed out that these results are strongly related to $\bar{a}$ parameter values, which were arbitrarily defined. They are in the same range of maximum catches obtained by using a multiple-linear relationship between effort, wind speed and CPUE, i.e., a family of Schaefer's model (1957). However, they turn out to be only indicative. Nevertheless, the models allow a look at three main eventualities, from the present situation.

(i) If wind intensity remains constant, any increase of fishing effort would not change the total catches but would reduce the CPUE.

(ii) If wind intensity increases (which seems hardly likely), CPUE and catches would increase, the exploitation rate (f/fMSY) would decline and profits will rise, even if the fishing effort slightly increases.

(iii) If wind intensity lowers significantly, then CPUE, and yield would decrease, meanwhile f/fMSY would increase without any f variation, from which a strong overfishing hazard may be produced.

Finally, it seems that fishing effort on Petite Côte has reached a critical level in biological terms, according to present environmental conditions. On the other hand, economical studies pointed out that artisanal fishermen using purse-seine (which assumes most of the catches) have very low profits due to existing commercial conditions. In spite of this situation, the number of fishing canoes shows a tendency to increase because the traditional distribution of gains privileges the owners of production materials and so, favours the increase in fishing units (Weber and Freon, in press). In consequence, artisanal fishing effort does not have a self-regulation mechanism and a new intensification of fishing effort on Petite Côte should be feared if wind intensity would decrease. This would lead to the catastrophic case where overfishing is likely. Moreover, the appearance in 1981 of a new tendency toward catching very small fish is also alarming.

It appears imperative to develop management decisions in order to limit the fishing effort growth on Petite Côte which could be done through a limitation of subsidies given for buying equipment and motor-fuel. The modification of traditional habits which favour the owner-minority seems difficult to realize. A more realistic solution lays in extension of the fishing grounds which are presently limited by the boat equipment and by the localization of landing sites. The Senegalese artisanal fishery, even enclosed in its social habits, is very open to technology innovations as demonstrated a few years ago by the successful introduction of outboard engines and afterwards by small purse-seines. In fact other areas of the Senegalese shelf are also very productive all year long (Casamance), or otherwise seasonal (north coast), but the absence of landing points and of commercialisation channels limits their full exploitation. Then it would be desirable to first, increase the range of canoes (diesel engines, fish preservation); second, improve fish distribution inside the country; third, renovate the old semi-industrial fleet; and fourth, provide small ports adapted to those boats.

On account of the important variability of the maximum catches related to environmental conditions, it is desirable to maintain flexible types of exploitation in order to allow quick adjustments to production fluctuations. So, the duality of the fishery (artisanal and semi-industrial) is of main interest.

Finally, it must be kept in mind that our models are based on a hypothesis which will not remain indefinitely true. The relative independance of the Petite Côte nursery will remain effective as long as the peripheral areas will not support overfishing. Otherwise, it would be inevitable that at a certain level the relationship between the adult sub-stock abundance and the Petite Côte recruitment will have a depressive effect on the latter. This situation will make obsolete our relatively optimistic models. Senegalese fishery management must be decided in concert with that of adjacent countries.

CONCLUSION

Modelling the whole sardine stock of the described West Africa area seems difficult presently due to the complexity of the population structure and to the data inadequacy in the Senegal adjacent countries. Anyway, under a certain hypothesis, it appears possible to establish production models for the Petite Côte sub-stock which is intensively exploited.

The model parameters obtained provide a satisfactory description of the fisheries evolution during the last 15 years which was mainly related to the fishing effort and to the upwelling intensity variations. However, the validity of the available data and the relative shortness of the observed period induce us to use only with care these models for forecasting purposes.

Presently, the sub-stock yield seems to be close to the maximum catch corresponding to the present wind intensity which is relatively high. In this situation, any fishing effort increase is unproductive and the only effect is a CPUE decrease. If wind intensity will decrease, the production would lower substantially, specially for sardine species. Of course, a wind intensity increase would be beneficial and would allow an effort increase without an overfishing hazard. Although it is difficult to forecast the wind speed, the available data from 1951 seems to indicate that this eventuality is more unlikely than the former one (Figure 10).

Fishery management actions should attempt to limit the present proliferation of fishing units on Petite Côte, especially artisanal ones. This objective can be reached on short term by enlarging the fishery area in latitude and toward the open sea. And finally, Senegalese management must be conducted in collaboration with adjacent countries. Only two of the three greatest dangers of collapse appears in the model equation (Petite Côte fishing effort and wind intensity). The last one, but not the least, is unfortunately hidden in our basic hypothesis (absence of overfishing in the adjacent areas).

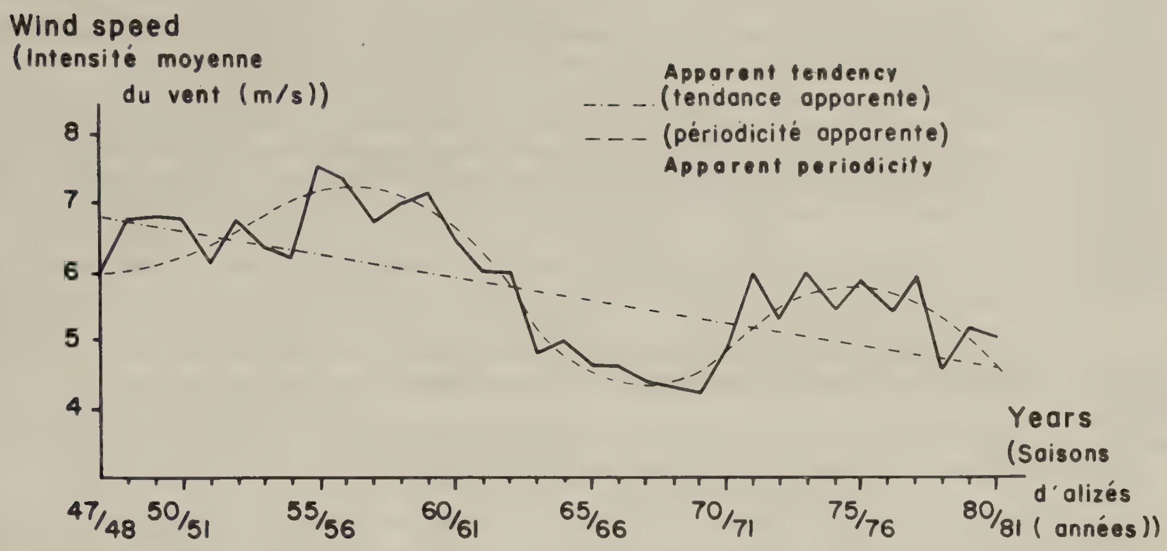


Fig. 10. Time plot of trade wind speed (meters per second) from 1947-1948 to 1980-1981 (data provided by ASECNA of Senegal and compiled by C. Teisson).

REFERENCES

Boely, T. 1980. Biologie des deux espèces de sardinelles (Sardinella aurita Valenciennes 1847 et Sardinella maderensis Lowe 1841) des côtes sénégalaises. Thèse Doc. d'état, Université de Paris VI:286 p.

Boely, T. and J. Chabanne. 1975. Les poissons pélagiques côtiers au Sénégal. La pêche sardinière à Dakar: état actuel et perspectives. Bull.IFAN. 37(Sér.A4):859-886.

Boely, T., J. Chabanne, P. Freon and B. Stequert. 1978. Cycle sexuel et migrations de Sardinella aurita sur le plateau continental ouest-africain, des îles Bissagos à la Mauritanie. Document présenté au CIEM/COI/FAO, Symposium sur le courant des Canaris: upwelling et ressources vivantes, Las Palmas, Espagne, 11-14 avril 1978. Commun. 92:12 p.

Boely, T., P. Freon and B. Stequert. 1982. La croissance de Sardinella aurita (Val. 1847) au Sénégal. Océanogr.trop. 17(2):103-119.

Champagnat, C. 1966. Indice relatif d'abondance saisonnières des Sardinelles de la Petite Côte du Sénégal. Doc.Scient.Provis.Centre Rech.Océanogr.Dakar-Thiaroye. (1):5 p.

Conand, F. 1977. Oeufs et larves de la sardinelle ronde (Sardinella aurita) au Sénégal: distribution, croissance, mortalité, variations d'abondance de 1971 à 1976. Cah.ORSTOM, ser.océanogr. 15(3):201-214.

Cushing, D.H. 1978. The problems of stock and recruitment. In Fish population dynamics (J.A. Gulland, ed.). John Wiley and Sons Ltd. 372 p.

FAO. 1980. Rapport du groupe de travail ad hoc sur les sardinelles de Côte d'Ivoire-Ghana-Togo. Tema, Ghana 2-7 Juillet 1979. Abidjan, Côte d'Ivoire 24-28 September 1979. COPACE/PACE Sér. (80/21) (Fa):73 p.

Freon, P. 1980. Choix d'une unité d'effort pour les flottilles sardinières semi-industrielles et artisanale du Sénégal. Doc.Scient.Centre Rech.Oceanogr.Abidjan. 11(1):1-35.

Freon, P. (In press). Des modèles de production appliqués à des fractions de stock dependantes des vents d'upwelling. Doc.Scient.Centre Rech.Océanogr.Dakar-Thiaroye.

Freon, P. and B. Stequert. 1979. Note sur la présence de Sardina pilchardus (Walb.) au Sénégal. Etude de la biométrie et interprétation. Cybium (3°Sér.). (6):65-90.

Freon, P., T. Boely and B. Stequert. 1979. Les pêches sénégalaises: description et analyse des captures et des rendements des principales espèces pélagiques côtières. In Rapport du groupe de travail ad hoc sur les poissons pélagiques côtiers ouest-africains de la Mauritanie au Libéria (26°N à 5°N). Dakar, Sénégal, 19-24 Juin 1978. COPACE/PACE Sér. (78/10):27-62.

Fox, W. 1970. An experimental surplus-yield model for optimizing exploited fish populations. Trans.Am.Fish.Soc. 99(1):80-89.

__________. 1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish.Bull.NOAA/NMFS. 73(1):23-36.

Harris, J.G.K. 1975. The effect of density-dependant mortality on the shape of the stock-recruitment curve. J.Cons.Int.Explor.Mer 36(2):150-157.

IOC. 1981. Workshop on the effects of environmental variations on the survival of larval pelagic fishes, Lima, 20 April-5 May 1980. IOC Workshop Report No.28. IOC/UNESCO, Paris. 323 p.

Marquardt, D. 1963. An algorithm for least square estimation of nonlinear parameters. J.Soc.Indust. and Appl.Math. 11(2):15-34.

ORSTOM. 1976. Rapport du groupe de travail sur la sardinelle (S. aurita) des côtes ivoireo-ghanéennes. Abidjan, ORSTOM, Centre de recherches océanographiques, 28 Juin-3 Juillet 1976:63 p.

Rebert, J.P. 1979. Un essai d'interprétation de l'influence des conditions de milieu sur les rendements de la pêches industrielle dakaroise de Sardinella aurita. In Rapport du groupe de travail ad hoc sur les poissons pélagiques côtiers ouest-africains de la Mauritanie au Libéria (26° à 5°N). Dakar, Sénégal, 19-24 Juin 1978. COPACE/PACE Sér. (78/10):105-108.

Roff, D.A. and D.J. Fairbairn. 1980. An evaluation of Gulland's method for fitting the Schaefer model. Can.J.Fish.Aquat.Sci. 37:1229-1235.

Rossignol, M. 1973. Contribution à l'étude du complexe guinéen. ORSTOM:142 p.

Saville, A. 1980. The assessment and management of pelagic fish stocks. A symposium held in Aberdeen 3-7 July 1978. Rapp.P.-v.Réun.Cons.Int.Mer. 177:517 p.

Schaefer, W.J. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull.IATTC. 2(6):85-245.

Sedykh, K.A. et al. 1978. Etude de l'upwelling près de la côte de l'Afrique nord-occidentale par l'Institut Atlantique de Recherches Scientifiques de l'Industrie de la Pêche et de l'Océanographie. In Rapport du groupe de travail ad hoc sur les poissons pélagiques côtiers ouest-africains de la Mauritanie au Libéria (25°N à 5°N). Dakar, Sénégal, 19-24 Juin 1978. COPACE/PACE Sér. (78/10):98-104.

Sissenwine, M.P. 1978. Is MSY an adequate foundation for optimum yield? Fisheries. 3(6):22-24 and 37-42.

Ulltang, Ø. 1976. Catch per unit of effort in the Norwegian purse seine fishery for atlanto-scandian (Norwegian spring spawning) herring. FAO Fish.Tech.Pap. (155):91-101.

Weber, J. and P. Freon. (In press). Djifère au Sénégal: la pêche artisanale en mutation dans un contexte industriel. 2° partie: Conséquences d'une innovation technique sur l'organisation économique artisanale, ou les excès d'une réussite. Doc.Scient.Centre Rech.Océanogr.Dakar-Thiaroye.

WHY DO SOME PELAGIC FISHES HAVE WIDE FLUCTUATIONS IN THEIR NUMBERS?

---BIOLOGICAL BASIS OF FLUCTUATION FROM THE VIEWPOINT OF EVOLUTIONARY ECOLOGY---

by

Tsuyoshi Kawasaki

Faculty of Agriculture
Tohoku University
1-1 Amamiya-cho
Tsutsumi-dori
Sendai-shi 980
Japan

Resumen

Los patrones de fluctuación en número de individuos varían de una especie (sub-población) a otra, los que han sido seleccionados a través del proceso de evolución. En el caso de teleósteos marinos se presentan tres tipos extremos de patrones de fluctuación, IA, IB y II, representados respectivamente por saury y amodites, arenque y sardina, atunes y peces planos. Una relación entre estos tres tipos puede ser expresada por un triángulo con dimensiones de longevidad, fecundidad y tasa de crecimiento.

El tipo IA, muestra cambios espaciados de breve tiempo, es una especie de vida corta, tiene una fecundidad baja, y el producto de k (parámetro de crecimiento de la ecuación de Bertalanffy) y T (tiempo generación) es bajo, lo que hace que la tasa instantánea de incremento natural de la población (r) sea alta, mientras que el tipo IB, se caracteriza por mostrar variaciones fenómenales de largo tiempo, son especies de vida larga, menos fecundas y el producto de kT es alto, y además acumulan una gran cantidad de peces cuando se presenta una sucesión de clases anuales fuertes a pesar de una r baja. El tipo II tiene una biomasa estable, son de vida larga, son más fecundos y el producto de kT, es bajo así como r. El patrón de fluctuación específico para esta especie depende mucho de las condiciones ambientales bióticas y abióticas en que se desarrolla la especie.

Las características de la ecología y el ambiente en que se desarrolla cada especie o su población tienen que ser tomadas en cuenta al momento de introducir medidas de ordenación de la pesquería. Se proponen medidas de ordenación para peces pelágicos y se hace una crítica de los modelos dependientes de la densidad en uso actualmente.

Los peces que se alimentan de plancton estan situados mucho más cerca a la fuente de energía solar, y por lo tanto parecen ser afectados fuertemente por los cambios del clima a través de los cambios océanicos. Esta observación puede ser válida en particular para sardinas, las que son casi exclusivamente herbívoras. El problema es que mientras en algunos años utilizan el fitoplánckton en forma eficiente, lo que da por resultado stocks muy grandes, en otros años no utilizan el fitoplancton tan eficientemente y se producen reducciones en su biomasa.

Aparentemente el patrón de vida de las sardinas cambia. Si las condiciones ambientales son favorables, las sardinas aumentan en número adoptando un modo de vida que les permite mantener su población a un nivel máximo posible. Por el contrario, si las condiciones ambientales de la sardina son adversas y su nicho ecológico se contrae, estas se preparan para el siguiente período de prosperidad asumiendo un estilo de vida en el cual se regula el crecimiento de la población.

INTRODUCTION

It has been well known that clupeoid fishes, especially the herrings and sardines, have phenomenal fluctuations in catch, viz. stock size. From of old, a variety of controversies have been held around the cause of such fluctuations and above all a dispute about the Californian sardine distributed off western North America is characteristic.

Stock size of the Californian sardine drastically declined after a peak in 1936 (Fig.1). The dispute around the collapse of the sardine stock has been continuing between scientists of California State standing on the conservation of the sardine stock and those of the Federal Government of the U.S. standing on the promotion of the fisheries (Radovich, 1981). In a paper jointly prepared by Clark and Marr (1955) each scientist reached an opinion different from the other based on the same data. Clark contended an influence of the exploitation on recruitments, saying that there had been a density-dependent effect between the stock and recruitment because if the stock size of the adult had been small, the resultant level of the progeny tended to become low. On the other hand, Marr asserted an effect of the environment on the recruitment, viz. density-independent effect, suggesting that the relation between the stock and recruitment was obscure.

The same circumstances as above have been seen in the Far Eastern sardine, the catch of which dramatically decreased after a peak in 1937 (Fig.1). Nakai (1962), a representative researcher on the sardine in Japan, tried to explain this event by the meandering of the Kuroshio. The stream axis of the Kuroshio, which flows eastward along the southern coast of Japan, often shifts, adding a semicircular southward movement. This in turn creates a counterclockwise cold eddy to the north and a clockwise warm eddy to the west. It is said that there are five types of pathway. One is normal or non-meandering (N), while the others meander in somewhat different patterns (types A-D in Fig.2). Although cold eddies associated with types B-D have occurred frequently, large-scale A-type fluctuations seldom have appeared.

Nakai (1962) presumed that the spawning of the sardine was concentrated on a region south of Kyushu, Japan, and their eggs and newly hatched larvae drifting eastward came across an A-type cold eddy, resulting in a mass mortality. On the contrary, Cushing (1971) regarded a disastrous decline in recruitment of the sardine resulting from the heavy fishing as a cause of the collapse of the stock.

While controversies between overfishing and natural cause around the decrease in stock of the sardines have been long held, similar disputes have also occurred about the herrings.

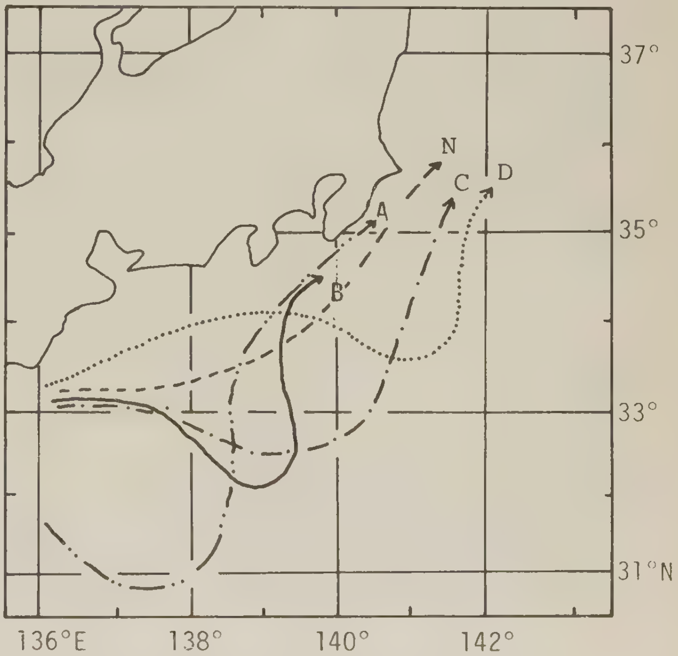


Fig.2. Types of meandering of the Kuroshio path south of Japan.

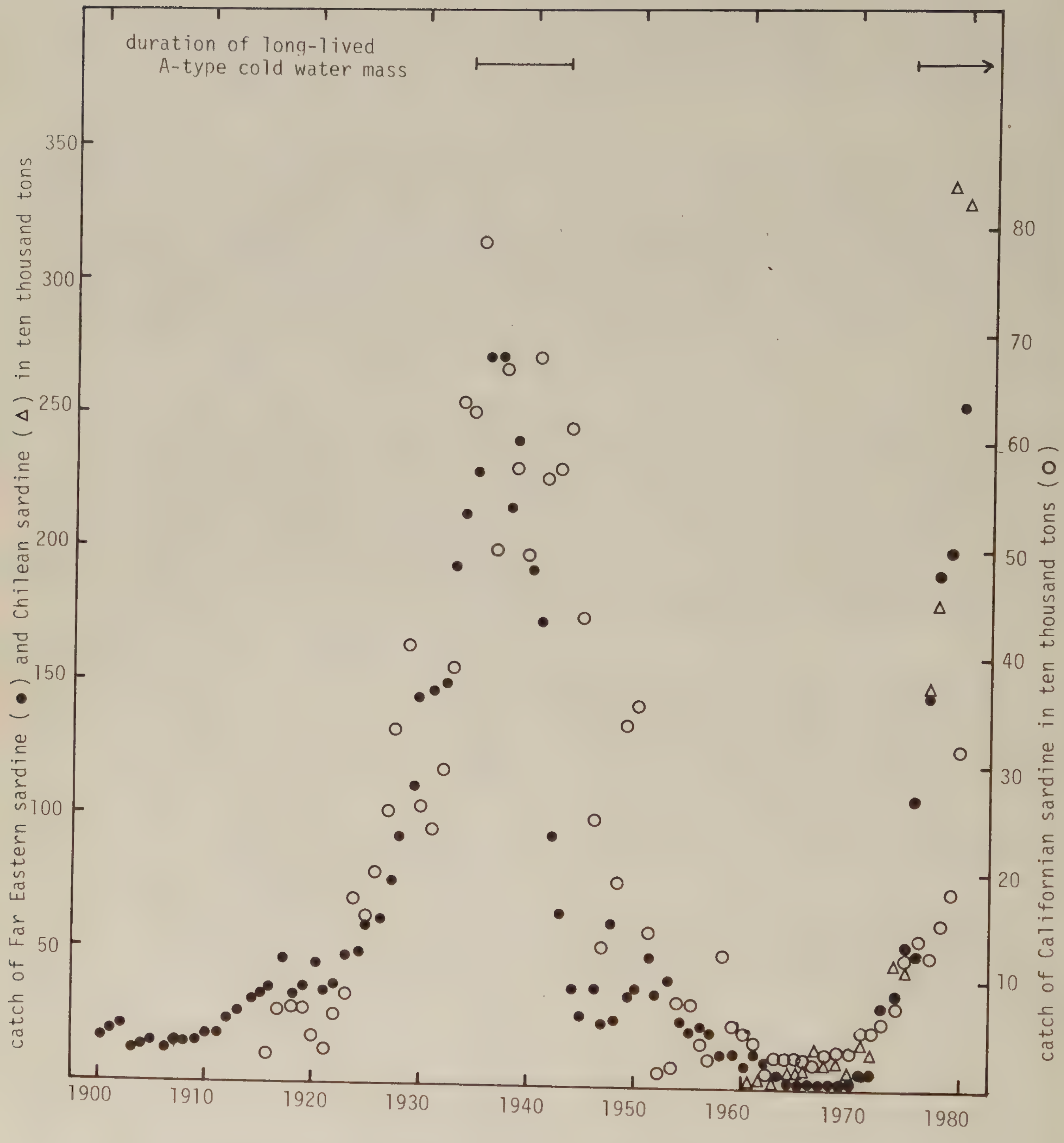


Fig.1. Large-scale variations in catch of three species of sardine, Far Eastern, Californian and Chilean.

CHANGE IN NICHE SIZE

The number of organisms of a species varies from generation to generation. Let us consider the meaning of this variation. That a species continue to survive means that the maximal quantity of the matter and energy possible are taken over from a generation to the subsequent one. According to Simpson (1952), the number of species currently existing is 2 millions, while that which have been extinguished to date is one half billion. This implies that most species failed to achieve persistant replacement from generation by generation, eventually disappearing from the earth. This also means that a small number of species could remain surviving at present. The author considers that the success or failure of the persistence of organisms (viability) from one generation to the next is closely linked with the status and problems involved in the ecological-niche in the community concerned. "Niche" is defined as the status of a species in a community composed mainly of predator-prey relations. This is provided by the overall biotic and abiotic environment surrounding the species. To maximize the quantity of surviving biomass between generations means that a species regulates its biomass so that the size of its niche is filled completely by its organisms. To regulate the biomass means to regulate the number of organisms. If a population does not increase sufficiently to fill its niche once it has been extended, this niche would be "violated" by another population, the niche of which is close to the former. On the other hand, if a population does not decrease its biomass in response to the contraction of its niche, many organisms of that population would die or become weakened due to overpopulation. Only a species which had acquired the ability to regulate its number so that it fills the niche completely in response to fluctuations in niche size could have survived.

The response pattern to fluctuations in niche size depends on species. Therefore, the pattern of fluctuation in number differs from species to species and this is called species-specific pattern of fluctuation in number. The species-specific pattern of fluctuation in number is the pattern of resource utilization for a species, which is having been formed through evolution and history.

EXTREME TYPES AND DEVELOPMENTAL PROCESSES OF THE PATTERNS OF FLUCTUATION IN NUMBER

Patterns of fluctuation in the number of marine teleosts can be assigned to three broad types.

Type I:	unstable and unpredictable
Subtype IA:	irregular and short-spaced e.g. Pacific saury and Pacific sandlance
Subtype IB:	large-scale and cyclical e.g. sardines and herrings
Type II:	stable and predictable e.g. tunas and flatfishes

In what environments did these three types have evolved? Cushing (1975) summarized the longitudinal features of production in the ocean. In the higher latitudes, while the large-scale primary production occurs in a short time and the productivity is very high, the delay period between the trophic levels is long, resulting in low ecological efficiency. In other words, productivity is high, efficiency is low, and variability is large. On this occasion, the abundance of a few species large in biomass largely varies corresponding to the fluctuation in niche size and they alternate with one another at shorter intervals, illustrating a phenomenon known as "alternation between species". The structure of such a community is simple and the relation among species is lax.

On the other hand, while in the low latitudes the low and continuous primary production occurs, the delay period between the trophic levels is short, resulting in a high ecological efficiency. In this case, while the productivity is low, the efficiency is high. There are many species whose biomasses are small and remain stable. The structure of a community is complex and interspecific relations are keen.

Not only the high latitudes are productive in the ocean. The productivity is also high in the upwelling areas, coastal areas and vertically in the surface. Because the niche size varies greatly in these environments, the species that have the ability to change their numbers corresponding to the change in niche have taken hold in these environments. These species have to pour more substance and energy into reproduction rather than maintenance and growth of the body in order to secure their broods. This is Type I.

On the contrary, because the variation in niche size is small in a poor, efficient and stable environment, the species need not greatly change their numbers. In such species more substance and energy are used for the maintenance and growth and they have to cope with the severe interspecific competition. This is Type II.

Let us think about the features of environmental variation in the sea. The changes in the seas are considered to be a synthesis of the short-spaced variation, with intervals of one to a few years, occurring in a relatively small area and large-scale variations, with cyles of several decades to centuries, occurring in large ocean-wide areas. While Subtype IA which has evolved matching the former is sensitive to the local environmental variation and its niche size varies finely, the niche size of Subtype IB matching the latter fluctuates largely (Fig. 3).

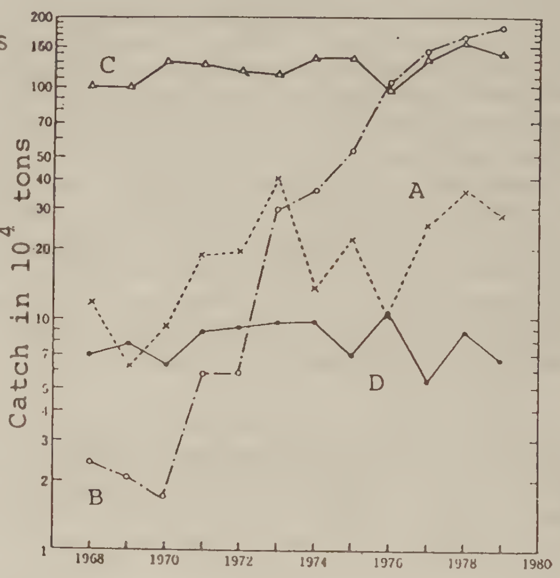


Fig.3. Inter-annual variations in catches of Pacific saury (A), Far Eastern sardine (B), chub mackerel (C) and albacore (D), caught in the Japanese fisheries.

Inter-relation among the three types

Subtypes IA and IB are not equivalent to each other and IA is the original pattern. Fish of Subtype IA have small body with short life, early reproduction and high intrinsic rate of natural increase *r*. They pour more matter from outside into reproduction by the quick alternation of generations in order to fully utilize their ecological niches, if they are extended by the betterment of environment or to cope with the contraction of their niches resulting from the deterioration of environment.

Whereas the life history type IA is optimal for a short-spaced environmental variation, it is not appropriate for a continuous long-period one, because in order to increase in step with the sustained extension of ecological niche, it is necessary to accumulate large year classes year by year, which in turn will produce larger year classes. Accordingly, this type of life history requires long life. However, to pour energy into reproduction, i.e. into the preservation of brood, is incompatible with long life.

A life history in which most growth is completed in an earlier period of life to begin reproduction as early as possible so that more energy is put into reproduction, has been selected as a way to overcome this contradiction. To reach the maximal size at a relatively young stage means that Bertalanffy's growth parameter *k* has a high value.

Since *k* has a dimension of reciprocal of time, *k* multiplied by cohort generation time, *T*, has to be used for comparison of growth patterns among species or subpopulations. As seen in Fig.4 values of *kT* are constant, on average, and a relation between the two parameters is hyperbolical (In Fig. 4 life span is used on behalf of *T*).

Fig. 4 also shows that all species and/or subpopulations of Genera *Sardinops* (sardines) and *Clupea* (herrings) close to Subtype IB, from 4 to 9 in the figure, have high *kT*'s, being situated above an arbitrarily drawn hyperbola.

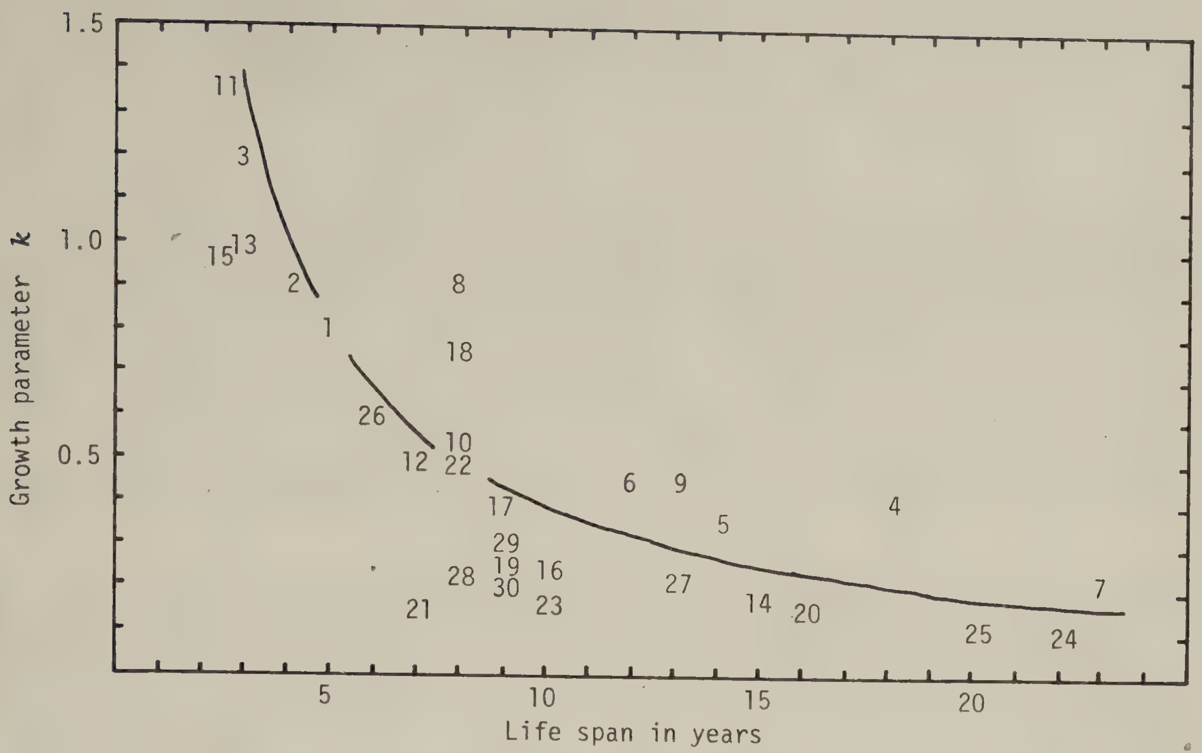


Fig. 4. Regression of growth parameter k on estimated life span, based on data from various sources. Numerals and a curve in the figure denote species number designated in Table 1 and arbitrarily adjusted hyperbola, respectively.

Table 1. Species numbers and names examined in Fig. 4

Order	Family	Species	
		Number	Name
Clupeiformes	Clupeidae	1	*Sprattus sprattus* (North Sea)
		2	*Sprattus sprattus* (Brittany)
		3	*Sprattus sprattus* (Spain)
		4	*Clupea pallasi* (Hokkaido-Sakhalin)
		5	*Clupea pallasi* (Okhotsk)
		6	*Clupea pallasi* (British Columbia)
		7	*Clupea harengus* (Atlanto-Scandian)
		8	*Sardinops melanosticta*
		9	*Sardinops caerulea*
		10	*Konosirus punctatus*
	Engraulidae	11	*Engraulis japonica*
		12	*Engraulis mordax*
		13	*Engraulis encrasicholus*
Anguilliformes	Muraenesocidae	14	*Muraenesox sinereus*
Atheriniformes	Scombresocidae	15	*Cololabis saira*
Gadiformes	Gadidae	16	*Theragra chalcogramma*
Perciformes	Sillaginidae	17	*Sillago sihama*
	Carangidae	18	*Trachurus japonicus*
		19	*Seriola quinqueradiata*
	Sparidae	20	*Pagrus major*
	Sciaenidae	21	*Argyrosomus argentatus*
	Scombridae	22	*Pneumatophorus japonicus*
	Thunnidae	23	*Thunnus alalunga*
		24	*Thunnus thynnus*
		25	*Thuunus maccoyi*
		26	*Katsuwonus pelamis*
Scorpaeniformes	Scorpaenidae	27	*Sebastes thompsoni*
Pleuronectiformes	Pleuronectidae	28	*Eopsetta grigorjewi*
		29	*Cleisthenes pinetorum*
		30	*Microstomus achne*

Fishes of Type II have large size and long life, growing slowly and becoming mature late. Thus they allocate more energy to maintenance and growth of the body.

Here, let us examine a problem concerning r where r is expressed as:

$$r \doteq \ln (\Sigma l_x m_x) / T$$

where l_x is the probability of female at age 0 of surviving to age x, m_x is the number of female eggs laid by the average female in the age interval (x - 0.5) to (x + 0.5). This equation indicates that r is positively proportional to the product of survivorship at ages producing eggs by fecundity and negatively proportional to the generation time, average ages of mothers, which is more influential on r than the former.

Subtype IA raises its r higher by shortening T as much as possible. Moreover, Subtype IA begins spawning as early as possible, effectively raising l_x by producing demersal eggs (in case of Pacific saury) or by their fathers caring for eggs by (in case of snailfish), and allows smaller body size, compensating any decrease in m_x resulting from short life. Thus, Subtype IA have acquired large r values like that of the Pacific saury as seen in Table 2.

Since r's in Subtype IB and II tend to become low because of their long T's, some life historical selections had had to be developed. Subtype IB either develops high GSI, gonad weight as a percentage of body weight (Fig. 5), or raises l_x as high as possible by laying demersal eggs (herrings), lowering the first age at maturity (sardines), etc. On the other hand, Type II has selected a strategy for higher m_x so that r does not become unnecessarily low. (Table 2).

Table 2. Some features of life history of four representative species

species	type	r	fecundity	egg diameter (mm)	age at maturity	mean age of mother	incubation time
Pacific saury	IA	0.921	10^3	1.31-2.08	1	1.5	8.5days(24°C)-33(10)
Californian sardine	IB	0.347	10^4	1.2-1.4	2	4.0	34hrs(20)-85(15)*
chub mackerel	II	0.245 - 0.285	10^5-10^6	0.9-1.3	3	4.2-4.9	30hrs(25)-97(15)
albacore	II	0.347	10^6	around 1	6	6.9	24hrs-38**

* Far Eastern sardine
** yellowfin tuna

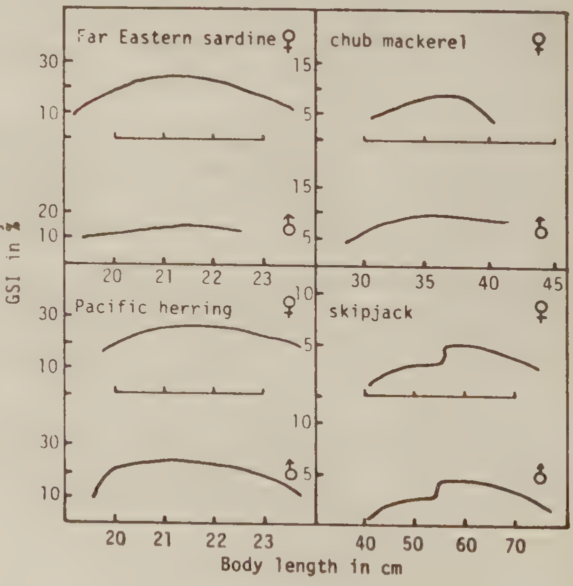


Fig. 5. Maximum-GSI- on-length curves for various marine teleosts. MBL denotes mean body length in mm of the data used, with number of fish in parentheses. F denotes fecundity.

Type II has selected two ways to produce a large number of eggs. One way is to obtain larger body size. Larger size has two advantages. One is to overcome competitors in severe interspecific struggles and the other is to increase available eggs. This is accomplished by keeping egg size small. As the present author (1978) pointed out, egg size of most marine teleosts falls within the range of 0.6 - 1.6 mm in diameter. Whereas a number of species under 50 cm in length have eggs larger than 1.6 mm, there are few species over 50 cm with such large eggs.

This way of life historical selection is found in the series from the Far Eastern sardine (*Sardinops melanosticta*) to skipjack (*Katsuwonus pelamis*) by way of chub mackerel (*Pneumatophorus (Scomber) japonicus*) (Fig. 5). In this series, whereas the difference between the sexes is small in respect to body size and GSI, the larger the body size becomes the more the fecundity increases and the less the GSI decreases. Decrease in GSI means that more subtance is poured into growth and maintenance, while absolute size of gonads increases.

The selection in this direction is seen in the migratory pelagic fishes. In these species sexual differences are small because fish of the same age must be of uniform swimming ability and the abundant male reproductive matter is necessary due to inefficiency of fertilization.

Another way to prevent reduction in r is to make the body size of female larger and its life longer as compared with those of male. This means that more matter and energy are allocated to female. Results of this type of selection are seen in Alaska pollack (*Theragra chalcogramma*) slime flounder (*Microstomus achne*) and others in Fig. 6. In this series the male lessens its size as well as its GSI. Selection in this direction is found in the less migratory demersal fishes. In this case, a small amount of male reproductive substance is able to fertilize a large quantity of eggs, as evident from the quasi-mating behavior of the slime flounder observed by Sato (1960).

The three types are the extremes and absolute examples may not exist in reality. A relationship among these three types is expressed in a life history triangle and a given species or subpopulation is to be situated somewhere in this triangle, as exemplified in this figure (Fig. 7).

In the life historical triangle (A) of Fig. 7, side IA-II represents a sexual dimorphism scale. In this figure an arrow toward Vertex II indicates that the females becomes larger than males. This is a direction taken by the heterosomes that live long and lay a large number of small eggs. There is another, oppositely directed arrow toward the snailfish and some gobies which are short-lived and produce a small number of large eggs cared for by their fathers.

Along side IA-II the nearshore and demersal fishes occupy their positions, while the domain from IA to II by way of IB is occupied by the pelagic fishes. Over side IA-II GSI is higher in the female than the male because the males of the nearshore or demersal fishes are able to fertilize the eggs more efficiently through various measures than are pelagic fishes that spawn in open surface or subsurface layers.

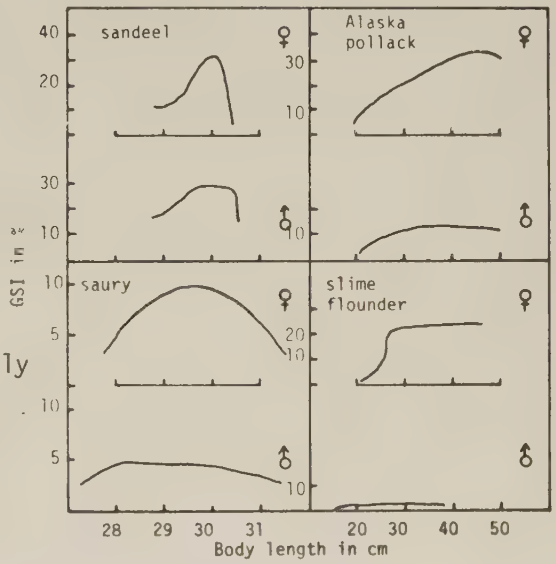


Fig.6. Maximun-GSI- on-length curves for various marine teleosts. For explanations, see Fig. 5.

On the other hand, Pacific saury, a species close to IA, occupies a position along side IA-IB, because this fish is a pelagic "swimmer" and exhibits little sexual dimorphism.

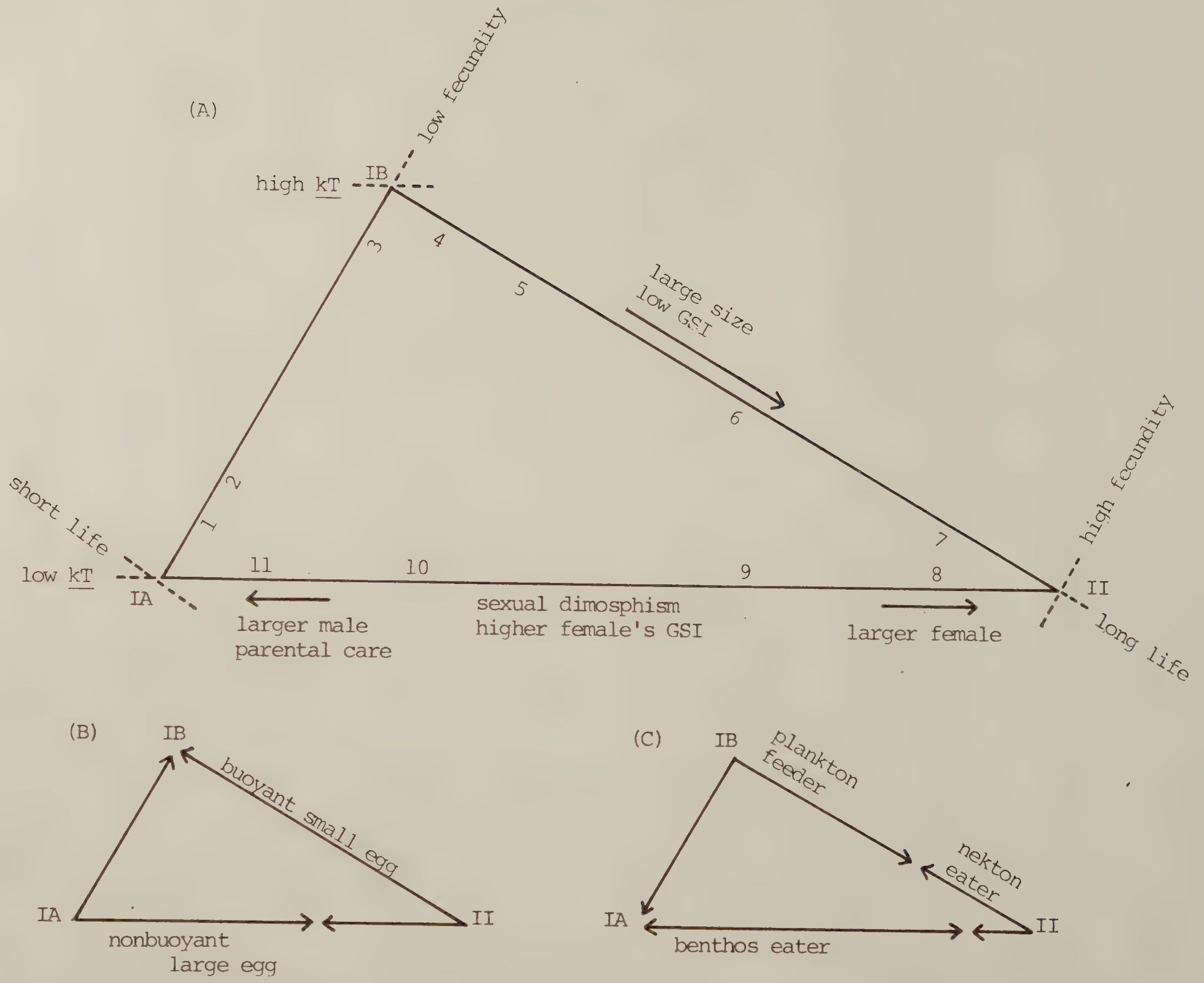

(A)
low fecundity
high kT
IB
3
4
5
large size
low GSI
6
high fecundity
short life
2
1
7
low kT
IA
11
10
9
8
II
long life
larger male
parental care
sexual dimosphism
higher female's GSI
larger female
(B)
IB
buoyant small egg
IA
II
nonbuoyant
large egg
(C)
IB
plankton
feeder
nekton
eater
IA
II
benthos eater

Fig.7. Life historical triangles of the marine teleosts, from the viewpoint of three dimensions (A), nature of eggs (B) and food habit (C). Number inside the figure (A) denotes locus of each taxon shown below.
1:saury, 2:sandlance, 3:herring, 4:sardine, 5:jack mackerel, 6:mackerel, 7:tunas, 8:heterosomes, 9:gadoids, 10:gobies, 11:snailfish

A part from vertex IB halfway to II by way of IA in (B) is a domain occupied by species depositing demersal large eggs, while that from IB halfway to IA via II is one occupied by fishes laying pelagic small eggs. Therefore, the sardines (*Sardinops*) and herrings (*Clupea*), both occupying loci close to IB, are located along side IB-II in (B) and side IB-IA respectively (Fig.7).

Benthos eaters are located between IA and a point a little apart from II in (C). From the latter point to one close to II on the way from II toward IB the nekton eaters are located (Fig.7). Among the benthos and nekton eaters interspecific competition for food can be keen. This is a domain efficient in food utilization and relatively low in biological production. On the contrary, a part from IA to a point near II by way of IB in (C) is occupied by the plankton feeders where interspecific interactions over food are lax. This is an inefficient and productive domain.

The correlates of three selected types of life history are summarized in Table 3.

Table 3. Correlates of three selected types of life history in marine teleosts

	Type I			Type II
	Subtype IA		Subtype IB	
Environment	Irregular variation	Variable and unpredictable	Long-term variation	Stable and predictable
Recruitment	Irregular variation	Variable	Long-term variation	Stable
Resources put into	Reproduction	Reproduction	Reproduction and maintenance	Growth and maintenance
Lifetime	Short		Long	Long
Growth				
kT	Low		High	Low
L_∞	Small		Moderate	Large
Reproduction				
Age at maturity	Very low	Low	Considerably low	High
Fecundity	Low		Moderate	High
r	High		Low	Low
Early survival		Variable		Stable
Trophic level		Low		High
Species close to each type	Saury, snailfish sandlance		Sardines, herrings	Tunas, flatfishes

Patterns of fluctuation in the number of the three types

The variations of the three types are represented diagrammatically in Fig.8. The figure employs the assumption common in population biology that variation in stock size can be represented by a logistic model. Expressing the carrying capacity of the environment K under favorable environmental conditions as K_2, and under adverse conditions as K_1, the stock size is to increase when K goes from K_1 to K_2 and to decrease when K declines from K_2 to K_1.

More formally,

$dN/dt = rN\,(K_2 - N)/(K_2 - K_1)$ representing the increasing phase ($K_1 \rightarrow K_2$)

$dN/dt = rN\,(K_1 - N)/(K_2 - K_1)$ representing the decreasing phase ($K_2 \rightarrow K_1$) $K_1 \leq N \leq K_2$

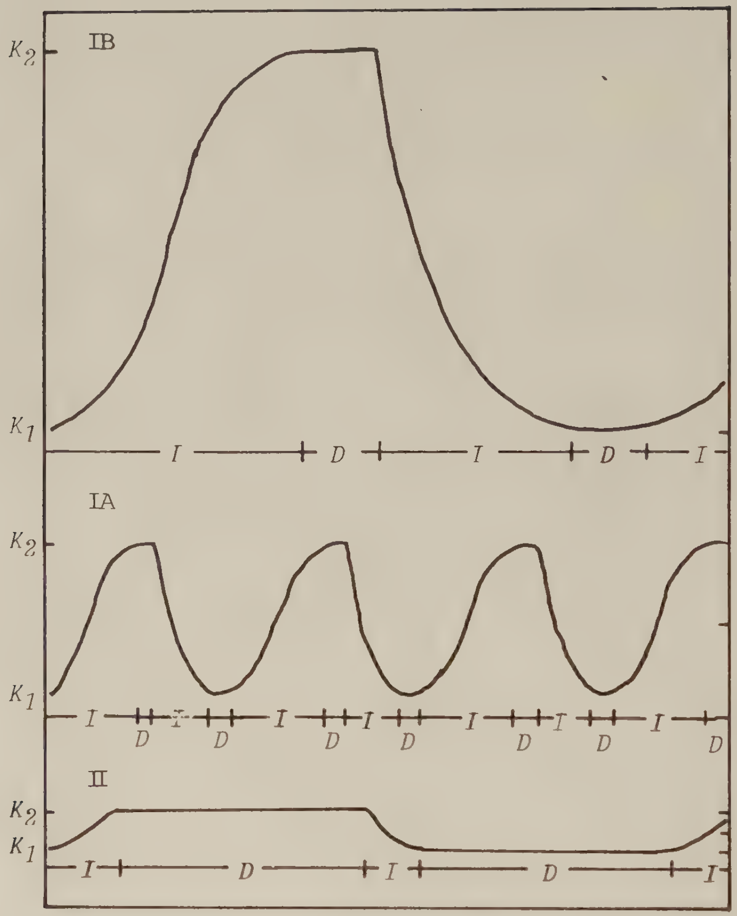

IB
K2
K1
I
D
I
D
I
IA
K2
K1
I
D
I
D
I
D
I
D
I
D
I
D
I
D
II
K2
K1
I
D
I
D
I

Fig.8. Three types of patterns of fluctuation in number of marine teleosts.

K_2 : high K K_1 : low K

D : Period when density-dependent factors work in the main.

I : Period when density-independent factors work in the main.

As seen in Fig.8, the values r and K_2 - K_1 are inherent attributes of a species and vary from species to species, even if they inhabit a common area. In Fig.8. I denotes periods when the density-independent factors (environmental factors) are the main influence, while D denotes periods when the density-dependent factors (biological factors) are the main influence. Duration of I is long and D is short for Type I species, indicating that they are apt to be subject to environmental change. In contrast, duration of I is short and D is long for Type II species, indicating that they tend more to be influenced by overfishing.

LARGE-SCALE FLUCTUATION OF THE THREE SARDINE STOCKS IN THE PACIFIC

Since the plankton-feeding fishes are situated close to the solar energy, they seem to be strongly affected by climate change through ocean change. In particular this is valid for sardines which are almost exclusively herbivorous. The problem is that whereas in some years they utilize phytoplankton as food efficiently, resulting in large stocks, in some years they do not and their biomass declines.

As background to this fact it seems that a change in the life pattern of the sardines occurs. If environmental conditions become favorable for sardines, their numbers increase by assuming a mode of life to keep their population as large as possible. On the contrary, if enviromental conditions for sardines become adverse and their niche contracts, they prepare for the next prosperity period by assuming a life style in which population growth is regulated.

What oceanographical variation governs the above situation? Fig.1. displays the tremendous large-scale fluctuations in catch exhibited by three species of Genus *Sardinops*, the Far Eastern sardine, Californian sardine and Chilean sardine. While these species are in the northwest, northeast and southeast parts, respectively, of the Pacific Ocean, their fluctuations are in phase with one another.

Nishimura (1980) said that the Far Eastern and Californian sardines are twins of a Japan-Oregon element and a species which had evolved off the west coast of North America and subsequently divided into two different species. I imagine that a part of the original species had further proceeded south and became the Chilean sardine. Three sardines are triplets, aren't they?

It would be impossible to explain the cause of a common fluctuation of the three sardine stocks without taking account of the Pacific-scale oceanic variations and related climatic changes.

While the links between ocean and atmosphere are easily recognized at a local and regional scale, there may also be identifiable interactions at a large scale. So-called "teleconnections" (Wyrtki, 1973), which shows significant relations of variations between very distant areas of the ocean and atmosphere, have been a subject of considerable study.

For example, originally it was believed that El Niño occurred when the local winds over the coastal upwelling zone became anomalously weak. According to Thompson (1981), however, there now is considerable evidence suggesting that basin-wide atmospheric and oceanographic anomalies are at least as important as the local winds in creating El Niño (Fig.9). Equatorial trades were unusually strong in 1970 and 1971, but were unusually weak in 1972. Furthermore, the eastward flowing North Equatorial Countercurrent intensified and the South Equatorial Current weakened during the 1972 El Niño. It appears that warm water accumulated in the eastern Pacific, deepening the usually shallow thermocline and covering the cooler upwelled waters. The local coastal winds along the Peru coast during the same period were normal or only slightly below normal.

Teramoto (1981) notes teleconnections between the following items: precipitation and cloudiness on Canton Island (3^oS, 172^oW) and Ocean Island (1^oS, 169^oE) in the central equatorial Pacific and the difference between water levels of northernmost and southernmost areas across the North Equatorial Countercurrent as an index of the current; the above difference between water levels and El Niño, using water temperature in the eastern equatorial Pacific as an indicator; the difference between water levels and longitudinal components of the velocity of geostrophic winds on a 700 mb plane along 30°N latitude (Fig.10). Statistical analysis suggests that these indicators lag one another by three to eight months. This same series of teleconnections also seems to be associated with the variation of the Kuroshio.

If the above discussion on large-scale ocean changes is valid, it is understandable why the three sardine species have shown almost identical trends of variation in stock size.

A long-lived A-type cold water mass may be regarded as a local manifestation of large-scale variation (Teramoto, 1981), such as occurred in 1934-1943 and has been occurring since 1975 to the present, a period when sardine stocks have been most abundant (Fig.1).

Such large-scale fluctuation exhibited by sardines depends upon their ecological features. They are long-lived, fast growing, direct herbivores in the coastal area, and these features mean that they are especially subject to changes of oceanic conditions. To summarize, large-scale fluctuation of *Sardinops* is caused by global-scale environmental variation and depends on whether the sardines are able to utilize a large quantity of phytoplankton or not.

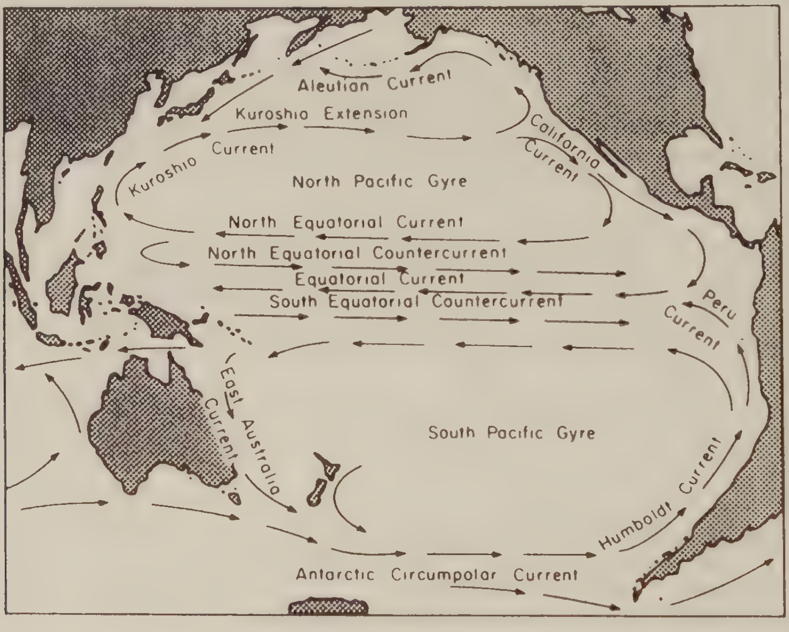

Aleutian Current
Kuroshio Extension
Kuroshio Current
North Pacific Gyre
California Current
North Equatorial Current
North Equatorial Countercurrent
Equatorial Current
South Equatorial Countercurrent
Peru Current
East Australia Current
South Pacific Gyre
Humboldt Current
Antarctic Circumpolar Current

Fig. 9. The current pattern in the equatorial region of the Pacific is more complex than that of the Atlantic, although to north and south similar enclosed circulatory gyres are formed. Recent research designates three west-flowing equatorial currents separated by two east-flowing equatorial countercurrents. (Courtesy Rand McNally Atlas of the Ocean.)

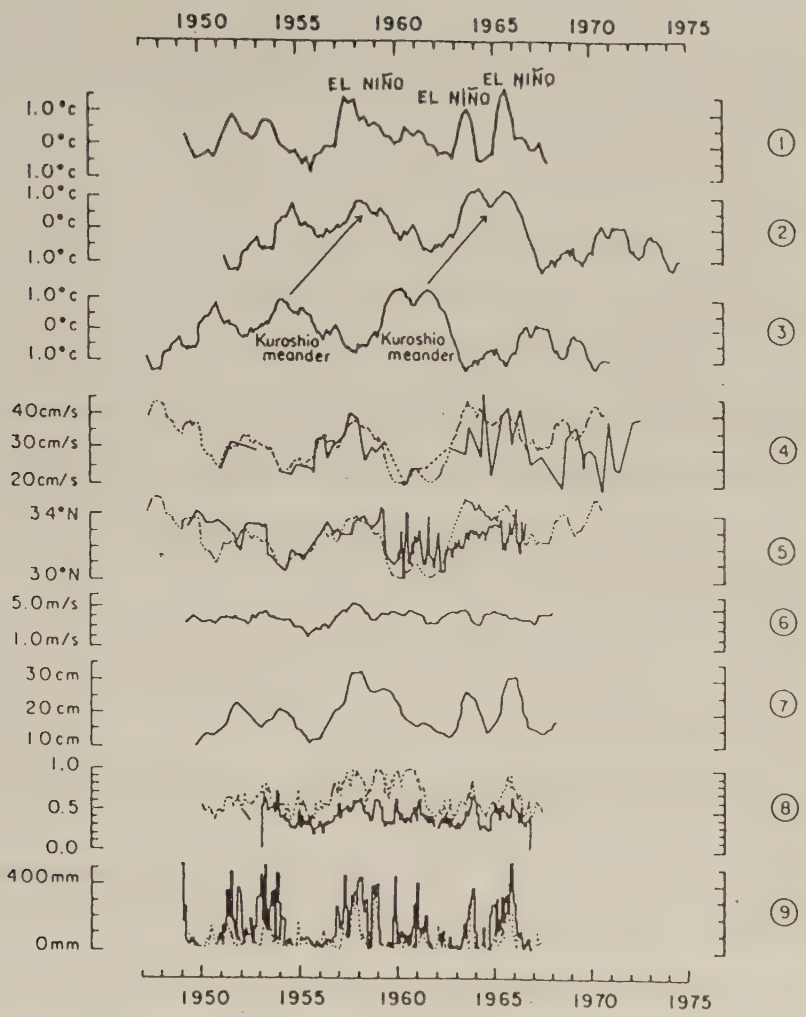


Fig. 10. (1) Anomaly of yearly mean water temperature on the coast of Central America.
(2) Anomaly of yearly mean water temperature on the coast of Izu-Oshima Island south of Honshu, Japan, delayed by some 4.2 years.
(3) Anomaly of yearly mean water temperature on the coast of Izu-Oshima Island south of Honshu, Japan.
(4) Mean of surface current velocity in the profile of the Kuroshio south of Cape Omaezaki, Japan (solid line), and inversion of (3) (dotted line).
(5) Stream axis of the Kuroshio south of Cape Omaezaki (solid line) and inversion of (3) (dotted line).
(6) Annual mean of the strength of westerly wind on a 700 mb plane.
(7) Variation in annual mean of differences between water levels across the Equatorial Countercurrent.
(8) Monthly mean cloudiness above Ocean Island (solid line) and that above Canton Island (dotted line).
(9) Monthly annual precipitation on Ocean Island (solid line) and that on Canton Island (dotted line).
(Teramoto, 1981)

REFERENCES

Clark, F.N. and J.C. Marr. 1955. Population dynamics of the Pacific sardine. Calif.Mar.Res.Com., Prog.Rep. 1 July 1953 to 31 March 1955.

Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J.du Cons. 33.

___________. 1975. Marine Ecology and Fisheries. Cambridge Univ.Press, Cambridge.

Kawasaki, T. 1978. Fluctuation in population of the marine teleosts. Kaiyo Kagaku (Marine Science), 10 (in Japanese).

Nakai, Z. 1962. Studies relevant to mechanisms underlying the fluctuation in the catch of the Japanese sardine, Sardinops melanosticta (Temminck and Schlegel). Jap.J.Ichthy. 9.

Nishimura. S. 1981. Ocean and Life on the Earth, Kaimei-sha, Tokyo (in Japanese).

Radovich, J. 1981. The collapse of the California sardine fishery: What have we learned? pp. 107-136. In Resource Management and Environmental Uncertainty. (M.H. Glantz and J.D. Thompson, eds.) John Wiley and Sons, New York.

Sato, Y. 1960. Spawning behavior of the slime flounder (preliminary report). Sokouo Joho, 26 (in Japanese).

Simpson, G.G. 1952. How much species? Evolution, 6.

Teramoto, T. 1981. Long-term variation of the Kuroshio. Kisho-Kenkyu Note (Meterological Research Note), 1412 (in Japanese).

Thompson, J.D. 1981. Climate, upwelling, and biological productivity: Some primary relationships. pp. 13-34. In Resource Management and Environmental Uncertainty. (M.H. Glantz and J.D. Thompson, eds.) John Wiley and Sons, New York.

Wyrtki, K. 1973. Teleconnections in the equatorial Pacific Ocean. Science. 180:66-80.

CHANGE IN ABUNDANCE AND SPECIES COMPOSITION OF NERITIC PELAGIC FISH STOCKS IN CONNECTION WITH LARVAL MORTALITY CAUSED BY CANNIBALISM AND PREDATORY LOSS BY CARNIVOROUS PLANKTON

by

Tomoyasu Kawai and Kimiko Isibasi

Tokai Regional Fisheries Research Laboratory
5-5-1 Kachidoki, Chuo-ku
Tokyo, Japan

Resumen

Se propone una hipótesis de trabajo sobre la mortalidad de las larvas causada por canibalismo y predación por parte del plancton carnívoro y el rol que tiene en los cambios en la abundancia y en la composición por especies de los stocks de peces neríticos pelágicos. Se ha llegado a la derivación de esta hipótesis a través de la investigación de varias características ecológicas importantes que son inherentes a cada especie. En base a esta hipótesis se propone un modelo matemático que parece describir bastante bien los cambios en el número de individuos en determinada cohorte a través de su vida. Se discute la hipótesis de trabajo en conexión con los fenómenos observados en las aguas alrededor de Japón.

Es bien conocido que la capacidad de proliferar es una de las características biológicas prominentes de los peces, la que se manifiesta con la producción de huevos de tamaño comparativamente pequeño. Otra particularidad encontrada entre los peces es la falta de relación entre el tamaño de los huevos y el tamaño del individuo adulto, mientras que en otros animales ovíparos es común encontrar una correlación entre estas dos características, caso típico de las aves.

A pesar de este hecho, cada especie de pez alcanza un tamaño corporal definido alrededor de un año después de haber sido desovado, tamaño que determina el tamaño del individuo adulto inherente a la especie. Por ejemplo, la anchoveta japonesa crece sólo hasta 11 cm. en el primer año de vida mientras que el atun ojo grande crece hasta 55 cm. Los autores piensan que estos cambios en el tamaño derivan de las diferencias en la alimentación durante el estado larvario y el primer año de vida. Se concluye que los hábitos alimenticios tienen una fuerte correlación con los parámetros pertinentes del crecimiento y reproducción de los peces, tales como la fecundidad y la primera madurez.

Una de las características observadas en los cambios en la composición por especies en las aguas alrededor de Japón es que la dominancia ha ido cambiando a través del tiempo de una especie costera a otra, que ha estado distribuida en las aguas vecinas mar afuera. Los autores asumen que las especies que se encuentran mar afuera, que se caracterizan por una capacidad potencial de aumentar rápidamente, comienzan a hacerse más abundantes cuando las otras especies comienzan a disminuir (debido mayormente a las grandes pérdidas durante sus estados larvarios causados por la predación del plancton carnívoro) y finalmente cambia la dominancia.

Se examinó la relación entre las edades de varios estadios importantes de la vida de las cohortes de 30 especies principales de Japón. Se examinó la edad a la primera madurez (tm), edad máxima (tx) y la edad a la máxima biomasa de la cohorte (ts). Se encontró que la edad a la biomasa máxima (ts) es muy sensitiva a los cambios en la abundancia de la cohorte en relación con los cambios en mortalidad promedio.

El incremento de la mortalidad inevitablemente hace disminuir el valor de ts, que normalmente es mayor que tm y tiene un valor cercano a tm + (tx - tm)/3. Con el aumento de la mortalidad, ts disminuye y se aproxima a tm, lo cual indica el estado de deterioro de la cohorte, especialmente en lo que se refiere a la producción de la próxima generación. Los autores proponen que este tipo de enfoque, es decir la observación de ts, tm y sus cambios en cada cohorte existente, puede ampliar y extender las aplicaciones de los métodos tradicionales de evaluación y ordenación de pesquería. Se hacen también algunas recomendaciones para futuros estudios.

INTRODUCTION

There have been numerous phenomena recorded characterized by large changes in abundance and species composition of neritic pelagic resources in many parts of the world's oceans. The waters around Japan are not exceptional when dominance switched from one species to the other over the years. The latest and most drastic change observed in the region was the burst of Japanese sardine and the change in the dominance from chub mackerel during the latter half of the 1970's. The catch of Japanese sardine has greatly increased since the early 1970's and is now more than 3 million tons, accounting for about 50 percent of the total pelagic fish production in the region, while the total production has been rather stable at about the 5-6 million tons level during the past decade. It has generally been extremely difficult to analyze the large and dramatic changes in the stock abundance and species composition of neritic pelagic fish resources. A reasonable explanation of the phenomena observed, or a prediction for future changes, has scarcely been made so far. The authors suspect, for the reason that some of the key factors which play an important role in these phenomena, have not been appropriately covered by the traditional methods of stock assessment, and the analysis of the entire mechanism has eventually remained beyond the conventional approaches carried out so far.

The authors think that more careful attention should be given to the biological-ecological factors during the early stages of life, especially on fecundity, growth and feeding habits. This idea has been derived from the results of a series of comparative studies on many fish species including oceanic and demersal fish. The studies have finally come across with a new hypothesis on larval mortality. The authors propose, in this paper, the working hypothesis on the role of several important ecological characteristics, which are genetically inherent to each species, in the change in stock abundance and, accordingly, change in species composition. A mathematical model being based on the hypothesis is then proposed, which appears to describe fairly well the change in the number of fish in a given cohort throughout their life-span. Discussions on the working hypothesis in connection with the phenomena observed in the waters around Japan are subsequently presented.

The authors are greatly indebted to Mrs. T. Takahashi for her enthusiastic assistance given to them during the study. The authors are also grateful to Dr. S. Chikuni, Fisheries Department, FAO for the critical comments and assistance he has given to them.

REVIEW OF IMPORTANT BIOLOGICAL CHARACTERISTICS

The authors reviewed the biological characteristics which may be relevant to the change in stock abundance on a comparative basis among many fish species. The authors limited the field of this comparison within marine teleostei. Most of the basic information and data on marine teleosts used in this study have been cited, unless specifically referred to, from Matsubara et al., (1965). Medians were used by the authors for the parameters given with ranges in the original reports. The relevant data on the biological features of 75 species employed in the analyses are given in Appendix I at the end of this paper.

Relationship between egg and adult sizes

Attention was first drawn by the authors to the size of eggs in connection with the large fecundity of marine teleosts. The simple, but principal question which arose from our review study was: Why are the egg sizes generally small throughout the Super-Order including tunas, which attain the largest body size, although the eggs of most tunas are, more surprisingly, usually smaller than those of sardines?

It is a general rule among terrestrial oviparous animals that egg size is nearly proportional to the size of the adult stage. Hence, it is peculiar that no correlation occurs between the eggs and adult sizes in marine teleosts. The authors assume that this peculiarity must have resulted in response to and "correlation" with the environmental conditions in order to maintain species abundances at persistence levels during their struggle for existence. The above-mentioned relationships between egg and adult size are clearly shown in Figure 1 for selected species by the three categories currently living in or around Japan. The adult sizes referred to in this study are the means of largest size generally observed but not the maximum size recorded, see the notation in Figure 1 for the definition of egg size.

Kawai (1978a, b) carried out a series of statistical analyses to look into these characteristics in further detail. However, any of the examinations on the type and nature of eggs, taxonomic position and ecological situation of fish did not show significant linkage with the relationship between egg and adult size.

Discontinuity of growth from egg to adult stages

In order to compare the sizes of fish five critical stages were selected as (1) egg, (2) immediately after hatching, (3) one full year of age, (4) biological minimum, and (5) adult (largest size in a common sense as defined earlier). The biological minimum size referred to in this study is the average size of fish after the first spawning in their life. These stages generally appear to represent the important segments of fish life in terms of growth in length with the exception of the "one full year of age" which is arbitrary from an ecological point of view. The size at one full year of age has been chosen simply on the basis that the available data lack sufficient information on a more ecologically-meaningful stage and size during the immature periods. Data for the shorter-lived fish, lives shorter than 3 years, have been excluded from the comparison of the size at one full year of age to avoid any bias related to adult size and early maturity due to small size. In this examination only data from females has been chosen to represent the species if growth is different between sexes. Comparison of sizes has been made between each successive stage of the above-mentioned five stages and the results are shown in Figure 2.

The results clearly show that the highly significant positive correlationships exist between the sizes at (1) egg and larva, (2) age-1 and biological minimum, and (3) biological minimum and adult. However, it appears there is almost no substantial relationship, neither positive nor negative, between the sizes at larva and age-1. This implies firstly that a significant discontinuity in growth pattern exists during the first year of age after hatching, and secondly that the species-specific growth pattern which determines the adult size is established during the same period, for instance, anchovy attains about 42 times greater body size from 2.6 mm to 11 cm while big-eye tuna about 370 times from 1.5 mm to 55 cm. The authors believe this phenomenon, which appears to be quite common among marine teleosts but extremely unique among oviparous vertebrates, is really crucial for the growth of each species and also suspect this may play an important role in other ecological features of fish, including those closely or directly linked with the subject of this study.

What could be the major factors which determine, during the first year of life, the species-specific growth pattern throughout the rest of the life? The authors conceived that perhaps differences in the quality of food is the major factor contributing to the differences in growth. It is probable that the growth rate of a specific species could be considerably higher even in the very small stages if highly nutritious foods are taken selectively. Rapid growth (rapid increase in the sizes of body and internal organs) may also boost the larger quantity of food intake which surely accelerates the growth rate.

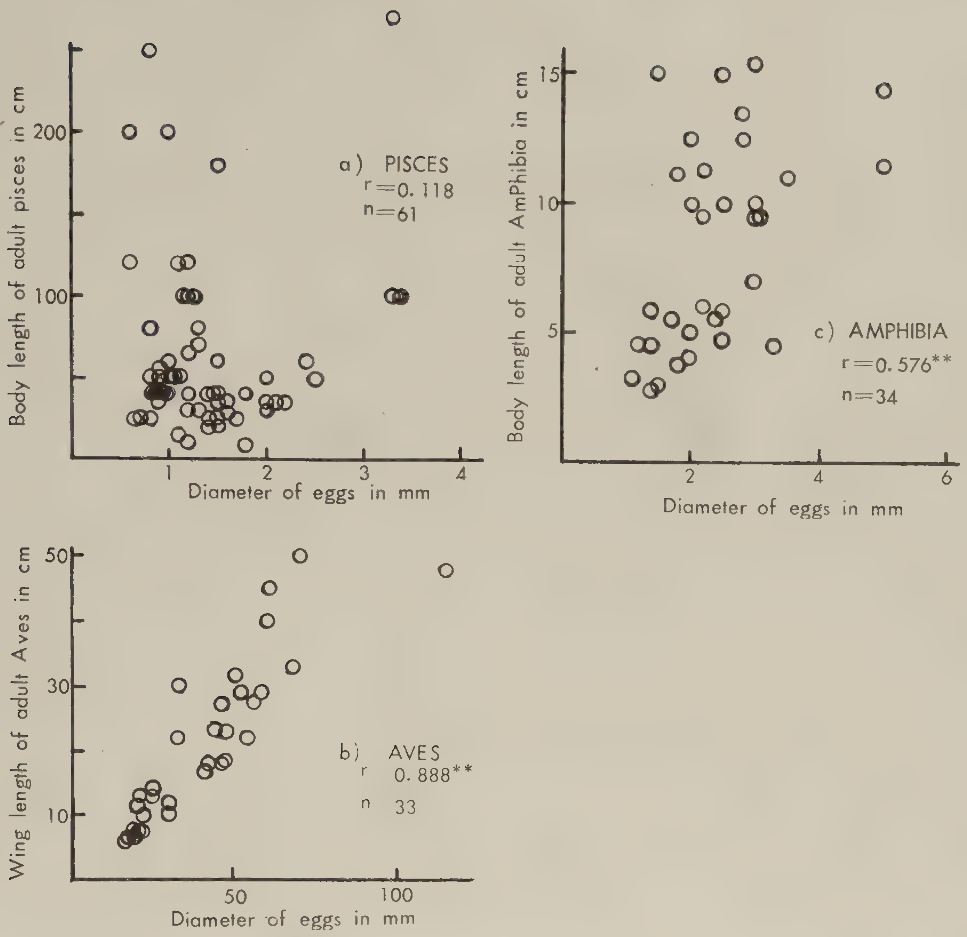


Figure 1

Relationship between the egg and adult sizes for selected species, examples: Pisces, Aves and Amphibia which currently live in or around Japan. The adult size means the largest size generally observed but not the maximum size recorded. The egg size referred to is the size of eggs at spawn. Means of the major and minor axes were applied for elliptical eggs with the exception of the Aves for which major axis was always applied.

r = correlation coefficient
n = number of sample

*, ** : significant at 5 percent or 1 percent, respectively, of the level of significance.

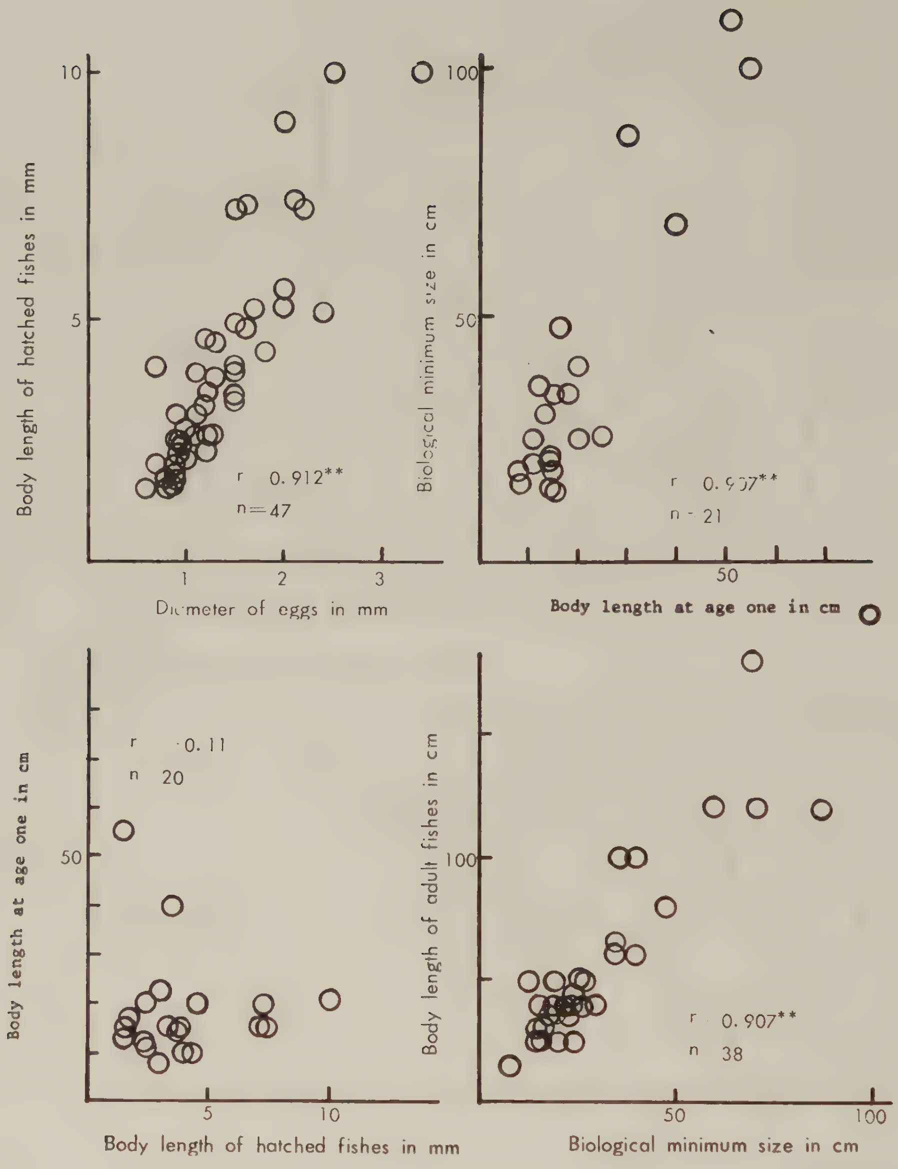


Figure 2

Comparisons of the sizes between two successive stages of life. See the text for the definition of each stage and Figure 1 for the notation in the figures.

Through choice of prey the larger species may thus have attained their specific growth patterns for the rest of their lives. The key factor or the trigger of the difference of growth could therefore be in the feeding habit which should have been genetically predetermined. In fact, it is well known that young fish generally attain the same feeding habits as their adult within the first year after hatching.

Relationship between growth and feeding habit and the implications to fertility

The species were categorized into three groups based on their feeding habits in adult stage which were mostly referred to Suehiro (1941). The planktivores and piscivores were clearly separated respectively and the remainder were all combined into one as omnivores as those species, e.g. benthos feeders, were rather difficult to categorize further into specific groups with such biological/ecological base as the first two. The comparison of body sizes at each growth stage among these species is given in Figure 3.

During the first two younger stages - egg and larva, there is no substantive relationship observed between the sizes and feeding habits though the planktivores show a slightly larger size than the other two groups. However, at the oldest two stages - biological minimum and adult, the difference in body size is clearly shown, that is, the largest are in the piscivorous group followed by omnivorous and the smallest in the planktivorous. It appears that the principle in these differences has been established by the end of the first year of life. It is also noted that the adult body size of the piscivorous group is prominent overwhelming the other two groups. These phenomena indicate that the discontinuity of growth patterns shown during the period starting from larvae to one full year of age was undoubtedly related to the differences in the feeding habits of each species.

These facts relate more importantly to the reproductive potential of any fish. Generally there is no large difference among fish species in the proportion of the ovary weight over body weight, which is usually about 12 percent (Kawai et al., 1981). It may therefore be a general rule that more eggs could be spawned by larger fish. This immediately suggests there is a larger fertility in piscivores. The authors assume that the fertility may have been one of the important rationales for piscivores attained throughout evolutional history. In other words, piscivores among marine teleosts might have evolved behind planktivores, specifically along the above mentioned pathway, though every teleost has perhaps strived toward its potential and opportunities to persist. The authors believe that distinction between planktivores and piscivores should be made in the population dynamics studies from this perspective.

Assumed implications of feeding habit to population dynamics

Through the analyses described so far, it has been assumed that piscivores may have evolved toward speeding up growth, but deferring age at maturity. This function is completely the reverse to the phenomena observed in an exploited or stressed single species population. For instance, Japanese sardine which grew slower and matured at age-3 during its prosperous period in the 1930's, speeded up their growth and became mature at age-2 when the stock abundance decreased during the 1950's. However, the authors believe that each of these two contradictory functions has its own biological rationale, considering the two different situations, i.e. the survival of species over the evolutionary long-term and compensatory reactions of a population against the short-term depletion in the latter case. It is assumed along these lines that the above-mentioned evolutionary tendency might have resulted in piscovores growing faster, attaining larger sizes and maturing at older ages which eventually promotes a larger fecundity with relatively small eggs. Enormous reproductive potential has thus been realized in many piscivores.

It is interesting to see, at the same time, that the spawning grounds of piscivores are generally located farther offshore than those of planktivores where nutrient conditions are undoubtedly poorer than in coastal waters. In contrast, the fecundity of planktivores is significantly less than piscivores. The authors believe however that there must again be a firm biological rationality even in these contradictory phenomena, and have come to assume that cannibalism of larvae by piscivores must be one of the major roles being played to resolve the nutrient deficiency problem. In fact, it is quite imaginable that larvae could be a source of nutrition to each other in the same population. This may have eventually functioned to stabilize more or less the magnitude of recruitment.

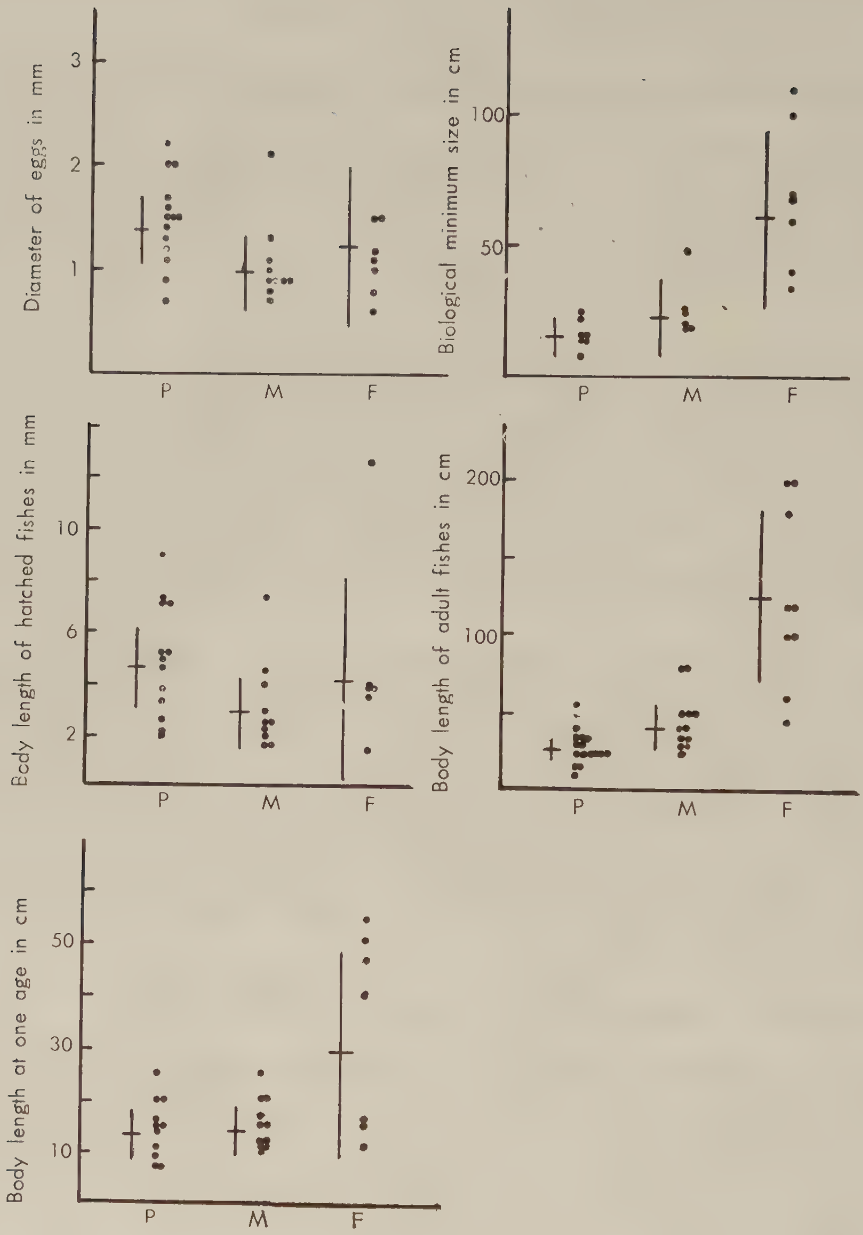


Figure 3

Comparison of body sizes at each growth stage among the groups categorized by feeding habit.

F : Piscivores, M : Omnivores. P : Planktivores.

The cross lines in each figure indicate the mean body sizes and the associated 95 percent confidence interval.

A NEW WORKING HYPOTHESIS ON LARVAL MORTALITY

The basic assumptions of the authors were: (1) the major cause of the loss of larvae must be the predation by something as larvae corpses are hardly seen in the sea, and (2) predators must be abundant to counter-balance the loss of larvae (Kawai et al., 1979, 1981). The hypotheses proposed for piscivores and planktivores are as follows:

Piscivores:

The important features of this species group to be taken into account are: (1) numbers of eggs spawned by each adult female is enormous, (2) spawning grounds are generally located in offshore waters where nutrient conditions are rather poor, (3) although egg size is comparatively small the size of the mouth of postlarva is relatively large and (4) stock abundances of adult piscivorous fishes are fairly stable in comparison to those of planktivorous fishes. The authors also assume that all larvae spawned would not necessarily starve to death in low nutrient offshore areas if larvae of the same species could be taken as feed. In other words, cannibalism must be the only way to survive for selected larvae and eventually sustains the existence of the species in such conditions. These features of this species category accords well with the authors' assumption and the hypothesis appears to have a plausible biological rationale in evolutionary contexts.

Planktivores:

The features of this species category are quite contrary to those of piscivores i.e. (1) numbers of eggs spawned by one adult female is relatively small, (2) spawning grounds are generally in coastal waters where plankton are abundant, (3) the mouth size of postlarva is very small and (4) the stock abundance of adult fish is generally accompanied by large fluctuations. Notable also is that the environment of coastal spawning grounds is usually unstable and unfavourable conditions sometimes occur for the larvae. However, more than 99 percent of the larvae spawned are definitely lost every year due to various reasons irrespective of the change in the environmental condition.

The authors hypothesize that the predation by carnivorous plankton would be the major cause of the loss of these fish larvae. It is strange to consider that planktivores are eaten by plankton at their larval stages, however, the authors think this phenomenon may also have biological rationale as such types of interactive co-existence are widely occurring.

EXAMINATION OF THE HYPOTHESIS

Larval mortality by cannibalism

It is well known that a massive death of larvae usually takes place during the so-called "critical period", very short period after feedings starts until attaining swimming mobility. The authors reviewed the morphological studies of the post-larvae of piscivores to investigate the feasibility of cannibalism among those larvae. Basic information employed here were cited from Shirota (1975) and Uchida (1958) in which the data on the sizes of body and mouth at post-larva stage are available for major fish species around Japan as shown in Table 1.

The proportion of mouth size against body size is generally about 10 percent, or about several hundred microns against several millimetres. However, the mouth size of piscivores is markedly larger than the others, mostly about 1 mm which is about double that of the others. Another thing notable in the comparison is that the mouth size is the largest in piscivores followed by omnivorous fishes and the smallest in planktivorous. The relative growth of upper jaw against body length shows a more interesting pattern by feeding habit of fish which is given in Figure 4 (Shirota, 1975). That is, skipjack and tunas (Group I) shows a sharp peak in mouth size at the earlier stage of post-larva which is followed by an obtuse peak at a slightly later period by Group II fish such as common mackerel, jack mackerel, yellowtail, red sea bream and sea bass whereas no such peak size is formed in anchovy (Group III) and saury (Group IV). It is the authors' view that the coincidence of the timing when mouth sizes become largest in Fish Group I and part of II, which are piscivores, with the timing of assumed cannibalims supports the proposed hypothesis well.

Table 1. Data on body length (L) and mouth size (D) in mm — diameter when mouth is opened - at post-larval stage of selected several species reported by two scientists separately (Shirota, 1975 and Uchida, 1958). The data have been re-arranged by the feeding habit of each species, namely:

P : Planktivores, O : Omnivorous, and F : Piscivorous

(A) Data reported by Shirota (1975)

Species	P			O			F		
	L	D	D/L	L	D	D/L	L	D	D/L
1	5.0	0.264	0.053	5.2	0.759	0.146	5.5	1.004	0.183
2	6.4	0.690	0.107	4.7	0.226	0.048	5.1	0.994	0.195
3	3.7	0.258	0.070	6.8	0.496	0.073	5.5	0.984	0.179
4	5.0	0.426	0.085	3.6	0.390	0.108	3.8	0.930	0.242
5	5.0	0.276	0.055	3.8	0.622	0.162	4.3	0.424	0.099
6	9.7	0.728	0.075	2.8	0.283	0.101			
7	4.4	0.291	0.066	6.6	0.882	0.134			
8	7.3	0.546	0.075	3.2	0.287	0.091			
9	9.2	0.550	0.060	2.8	0.223	0.079			
10	3.0	0.259	0.086	4.1	0.594	0.144			
11				3.6	0.303	0.084			
Number of Species	10			11			5		
Average	5.9	0.429	0.073	4.3	0.461	0.106	4.8	0.867	0.180

Species

P 1 : *Konosirus punctatus*
P 2 : *Etrumeus micropus*
P 3 : *Engraulis japonica*
P 4 : *Sardinops melanosticta*
P 5 : *Spratelloides japonicus*
P 6 : *Clupea pallasi*
P 7 : *Harengula zunasi*
P 8 : *Cololabis saira*
P 9 : *Hemiramphus sajori*
P 10 : *Oplegnathus fasciatus*

O 1 : *Mugil cephalus*
O 2 : *Ammodytes persanatus*
O 3 : *Ilisha elongata*
O 4 : *Trachurus japonicus*
O 5 : *Scomber japonicus*
O 6 : *Sillago sihama*
O 7 : *Girella punctata*
O 8 : *Siganus fuscescens*
O 9 : *Platycephalus indicus*
O 10 : *Chelidonichthys kumu*
O 11 : *Fugu rubripes*

F 1 : *Seriola aureovittata*
F 2 : *Seriola quinqueradiata*
F 3 : *Seriola purpurascens*
F 4 : *Katsuwonus pelamis*
F 5 : *Gadus macrocephalus*

Table 1 Continued

(B) Data reported by Uchida (1958)

Species	P			O			F		
	L	D	D/L	L	D	D/L	L	D	D/L
1	4.8	0.269	0.056	4.0	0.520	0.130	5.5	1.025	0.186
2	6.9	0.676	0.098	6.6	0.884	0.134	5.1	0.549	0.108
3	10.4	0.730	0.070	3.3	0.236	0.072	5.5	1.007	0.183
4	5.9	0.508	0.086	3.6	0.318	0.088			
5	4.4	0.372	0.085	4.1	0.614	0.149			
6	7.4	0.485	0.066						
7	10.7	0.550	0.051						
8	3.0	0.310	0.103						
Number of Species	8			5			3		
Average	6.3	0.488	0.077	4.5	0.514	0.115	5.4	0.860	0.159

Species

P 1 : *Konosirus punctatus*
P 2 : *Etrumenus micropus*
P 3 : *Clupea pallasi*
P 4 : *Sardinops melanosticta*
P 5 : *Harengula zunasi*
P 6 : *Cololabis saira*
P 7 : *Hemiramphus sajori*
P 8 : *Oplegnathus fasciatus*

O 1 : *Scomber japonicus*
O 2 : *Girella punctata*
O 3 : *Siganus fuscescens*
O 4 : *Fugu rubripes*
O 5 : *Chelidonichthys kumu*

F 1 : *Seriola aureovittata*
F 2 : *Seriola quinqueradiata*
F 3 : *Seriola purpurascens*

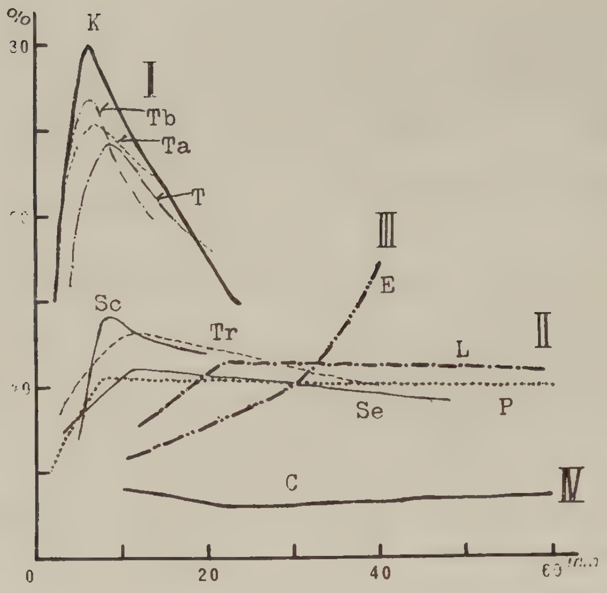


Figure 4

Relative growth of upper jaw against body length during larval and post-larval stages by the type of fish (Shirota, 1975).

Group I. T: *Thunnus thynnus*, Ta: *T. alalunga*, Tb: *T. albacares*, K: *Katsuwonus pelamis*

Group II. Se: *Seriola quinqueradiata*, Tr: *Trachurus japonicus*, Sc: *Scomber japonicus*, L: *Lateolabrax japonicus* P: *Pagrus major*

Group III. E: *Engraulis japonica*

Group IV: C: *Cololabis saira*.

Mathematical expressions:

The initial stock biomass (W_0) is given by:

$$W_0 = N_0 w_0 \qquad \ldots.(1)$$

where N_0 : initial stock number

and w_0 : body weight of a fish.

Assuming that all the brood hatch simultaneously and the stock weight changes due to cannibalism to the biomass W_1, (assumed to take place simultaneously),

$$W_1 = \frac{N_0}{2} w_0 (1 + r) = \frac{1 + r}{2} W_0$$

where r : food efficiency.

After a second cannibalism the stock biomass would be

$$W_2 = \frac{N_0}{2^2} w_0 (1 + r)^2 = (\frac{1 + r}{2})^2 W_0$$

hence the stock biomass after n-th cannibalism is given by:

$$W_n = \left(\frac{1 + r}{2}\right)^n W_o = Q^n W_o, \ (Q \leqslant 1) \qquad \ldots.(2)$$

The change in W_n against n for various r is shown in Figure 5.

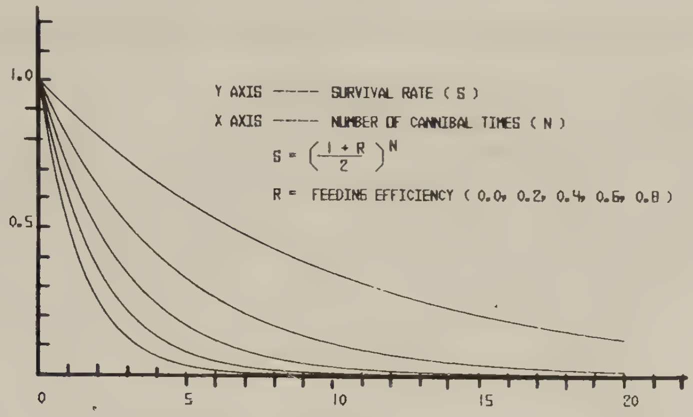


Figure 5

Change in the relative stock biomass over the initial stock biomass (W_n/W_o) against the number of cannibalism (n) for various values of feeding efficiency (r).

It may be appropriate to assume that the amount of food intake would be proportional to the time sequence, that is, the increase in the weight of larvae by rw_o by one cannibalism means that the $(1 + r)w_o$ food would be taken in at the next cannibalism. Assuming that the time interval among each cannibalism would be prolonged by $(1 + r)$ times, the timing of the n-th cannibalism (t_n) would be

$$t_n = d + d\,(1 + r) + d\,(1 + r)^2 + \ldots. + d\,(1 + r)^{n-2}$$

$$= d\left(\frac{(1 + r)^{n-1} - 1}{r}\right) \qquad \ldots.(3)$$

where d : initial time interval, $t_1 = 0$ and $r \ngtr 0$. Hence

$$n = \frac{\log\,(1 + r)(1 + \frac{r}{d}\,t)}{\log\,(1 + r)}$$

The time sequence function of the stock biomass is given by putting the above notation into equation (2)

$$W_t = W_o\left(\frac{1 + r}{2}\right)^{\frac{\log\,(1 + r)\,(1 + \frac{r}{d}\,t)}{\log\,(1 + r)}} = W_o'\,(1 + \frac{r}{d}\,t)^a$$

where $W_o' = QW_o$ and $a = 1 - \frac{\log 2}{\log\,(1 + r)}$, in another form:

$$W_t = \frac{W_o'}{(1 + \frac{r}{d}\,t)^b} \qquad \ldots.(4)$$

where $a \leqslant 0$ as $0 \leqslant r \leqslant 1$ and $|a| = b$. That is to say that the stock biomass (W_t) is noted as a negative power function of time sequence (t). A trial application of the above function was made to the data for yellowtail around Japan. Adopting that the r of yellowtail in rearing condition is about 0.25 (Ichimura, 1978) and assuming that the growth in length during the post-larva stage is about double, the increase in weight would be about 8 times. Therefore

$$W_n/W_o = (1 + r)^n = 8 \quad \text{and} \quad n = 9.3$$

This indicates that about 9-10 cycles of cannibalism would take place for the larvae which survived to the post-larval stage. The survival rate during the same period is accordingly estimated to be:

$$S = (\tfrac{1}{2})^{9.3} = 0.00159$$

which accords well with the global estimate of larval survival, about 1/1,000.

Larval mortality by predation by carnivorous plankton

It is well known that plankton play an important role in the food chain as the primary food for other animals in marine environment. The converse function i.e. the feeding by plankton on the eggs and larvae of fish has, in contrast, paid little attention to population studies. There have been, however, many records of predation of carnivorous plankton on fish larvae which made the authors propose their new hypothesis. Documental predators are, for example, medusae, ctenophora, chaetognatha and annelida on herring (Lebour, 1923), Noctiluca on anchovy (Hattori, 1962), Sagitta on sand lance (Hamada, 1965), jellyfish on sprat (Fraser, 1969) and copepod on anchovy (Lillelund et al., 1971).

The authors (Kawai and Ishibasi, 1981) estimated the relative abundance of four major carnivorous plankton species (Medusae, Polychaeta, Chaetognatha and Amphipoda) around Japan based on the data reported by Yamazi (1971). The result obtained was surprisingly large, about 15-20 times the abundance of fish eggs and larvae, and was implied by the large effect of predatory loss of fish larvae.

Mathematical expressions:

The stock number (N_t) and individual body weight (w_t) change during the critical period as

$$N_t = N_o e^{-Mt} \quad \text{and}$$

$$w_t = w_o + ct$$

where: N_o and w_o are initial stock number and body weight,

M : the natural mortality coefficient which may be proportional to the abundance of carnivorous plankton,

and c : coefficient of growth which may be proportional to the abundance of food. The stock biomass (W_t) is given from these formulae as

$$W_t = N_t w_t = W_o (1 + Gt)e^{-Mt} \qquad \text{....(5)}$$

where G denotes the rate of weight increments against the initial body weight (c/w_o) in which an approximation with linear growth function is applied here for the rather short time interval during the critical stage. To identify the changes in the stock biomass in connection with the changes in M, the following equations are derived from equation (5):

assuming:

$$\frac{dW}{dt} = W_o (G - M - MGt)e^{-Mt} = 0$$

the maximum stock biomass W_s and the time when W_s is realized are given by

$$t_s = \frac{1}{M} - \frac{1}{G} \qquad \text{....(6)}$$

$$W_s = \frac{G}{M} W_o e^{-(1 - \frac{M}{G})}$$

which implies that W_t converges to 0 as t approaches infinity. The coordinates of the turning point (t_h, W_h^t) are given by

$$t_h = \frac{2}{M} - \frac{1}{G}$$

$$W_h = \frac{2G}{M} W_o e^{-(2 - \frac{M}{G})}$$

The curves of W_t/W_o against t are shown in Figure 6 for various values of M.

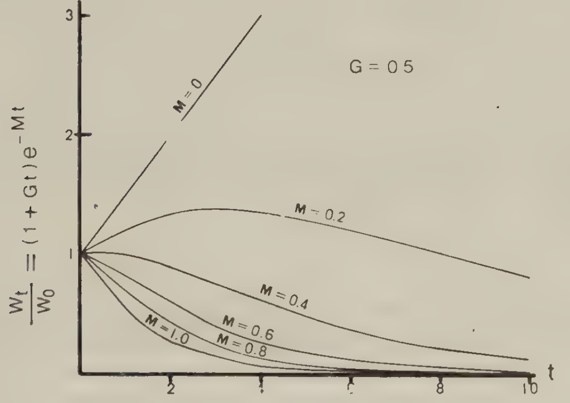


Figure 6

Change in the relative stock biomass over the initial biomass (W_t/w_o) against time sequence (t) for various natural mortality coefficient (M). G denotes the rate of weight increments over the initial body weight (c/W_o) where c is the coefficient of growth.

Equation (6) or Figure 6 shows that $W_t > W_o$ is realized somewhere under the condition of $M < G$ and vice versa. It is generally accepted in the natural condition that the probability on encountering with feed is larger than that with predator. The stock biomass might therefore be increased slightly to be $W_t > W_o$, which is quite in contrast with the case in cannibalism where W_t never increased, then $M < G$ would be realized which gives the condition of the upper limit of M. It is likely, on the other hand, that the stock biomass would decrease than the initial size (W_o) at the end of the critical period even though W_t increased somehow at the intermediate stages. The stock biomass at the end of the critical period (for the entire time interval of T) is given as

$$W_T = W_o (1 + GT)e^{-MT}$$

$$W_T < W_o \quad \text{hence}$$

$$M > \frac{1}{T} \log (1 + GT) \qquad \text{....(7)}$$

The above notation gives the condition of the lower limit of M.

The body length of larvae grows generally about double during the post-larvae period and the body weight grows accordingly to 8 times during the same period as

$$w_o + cT = 8\ w_o$$

hence

$$c = \frac{7}{T} w_o \quad \text{and} \quad G = \frac{7}{T}$$

the possible range of M is therefore given by

$$\frac{\log 8}{T} < M < \frac{7}{T}$$

or in survival rate (S), as

$$0.0009 < S < 0.125$$

since

$$S = \frac{N_t}{N_o} = e^{-MT}$$

The range of the survival rate obtained here for planktivores appears to be well balanced with that of piscivores (about 1/1,000) and also well balanced with the general information on the larval mortality of this type of fish.

Discussion of the hypothesis

It has been widely accepted by many scientists that several unfavourable conditions in the environment such as oceanographic or meteorologically bad conditions, lack of feed and predatory loss by other fish would be the major causes of larval mortality. It may be true that a combination of these factors may play substantive roles, however, the authors doubt whether these factors or the combination of them have definitely been the major causes for the larval mortality which definitely causes the 99 percent loss every year.

The relationship between the change in the oceanographic/meteorological conditions and the definite loss of fish larvae observed every year has remained very vague with the exception of a few special occasions such as drastic changes in upwelling, sea currents, sea-ice formation and water temperature etc.

It is generally said that the plankton biomass would be about 10 times larger than that of all the fish, including adults, to be supplied as feed. Even if we assume that the feed for fish larvae comprises mostly copepod nauplii, it is quite unlikely that an extraordinarily severe condition of food supply for fish larvae would occur every year to make 99 percent fish larvae starve to death when the fact that copepod biomass accounts for several tens percent of total plankton biomass is taken into account.

It is also reasonable to consider that the predatory loss to other fish would be one of the major causes of massive larval mortality. It may be unlikely that other fish would feed selectively on fish larvae during their critical period which is of a rather short duration, 2-3 months at most for the entire spawning period. Fish larvae may be taken by other fish together along with the other planktonic organisms. The massacre of fish larvae by only other fish is therefore quite unlikely to have happened considering the enormous amount of plankton biomass.

It is concluded that the above-mentioned environmental conditions are supplementary, though there is no doubt on the existence of substantial negative effects by them, and the authors have found it more reasonable to hypothesize that cannibalism among the same fish larvae and the predatory loss by carnivorous plankton would be the major causes of the larval mortality of piscivores and planktivores respectively. The former cause functions as a density-dependent factor while the latter as a density-independent factor, which also gives a logical coincidence with the facts that the abundance of piscivorous stocks fluctuate less than that of planktivorous.

APPLICATION OF THE HYPOTHESIS TO THE STOCK ASSESSMENT OF NERITIC FISH RESOURCES AROUND JAPAN WITH SPECIAL EMPHASIS ON THE CHANGE IN SPECIES COMPOSITION

Review of the change in species composition

The historical change in the species composition in the nominal catch of neritic pelagic fish is shown in Figure 7 by major sea region around Japan for the past 80 years. In the figure the component of each species is placed from the bottom to the top in accordance with their body size (smaller to larger), to enable the reader to understand the authors' discussion more easily thereafter.

Generally speaking, smaller species are located at a lower position in the food chain. In fact, the specimens of larger fish, even though smaller stages of them - larvae and fry - has scarcely been found in the stomach of smaller fish. A few examples of this type of phenomena is given in Figure 8, which shows clearly the predominance of larger species over smaller species. A notable phenomenon observed, in addition to the principles mentioned above, is that a certain size species depends not only on the species located just beneath but also all the species of ecologically lower levels. This is somewhat different in principle, from the hierarchy on species (compilation of dependency between the neighbouring two species - from top to bottom) which has been widely accepted by scientists so far.

Until around 1950 almost no substantial change in species composition was observed in the nominal catch record in each of the regions (Figure 7). This may partly be due to the fact that the fisheries and fishing activity before World War II were not sufficiently fully developed to reflect changes in resources by their catch. It appears, in contrast, that the recent fishing activities would reflect fairly well the change in the major components of the entire exploitable resource in accordance with the development of fishing techniques and the expansion of fishing grounds.

Secondly, it is noted that the change in dominance was taking place generally from smaller species to larger ones (from lower to upper in Figure 7), in each of the regions during nearly the same periods, although the specific species changed are different among the regions. For instance, the dominance was switched from (1) sardine-jack mackerel-mackerel in turn in the Western Japan Sea Region, (2) sardine-saury-mackerel in the Northern Pacific Region and (3) sardine-jack mackerel-mackerel in the Southern Pacific Region, which are all changes from smaller to larger species (lower to upper in Figure 7). The only exception is the recent burst of sardine observed again in each region which will be discussed later.

Among these, changes in the Southern Pacific Region are relatively moderate to the other two regions. The region is located at the southernmost area where the warm "Kuroshio" current prevails. The authors assume that the multi-species nature in warmer waters in the region is well represented in this phenomenon, which may have more or less stabilized any potential changes in species composition. The total amount of the pelagic fish catch in the Southern Pacific Region also shows the most stable trend among the three regions.

Hypothetical consideration on the change in species composition

As was mentioned above, the dominant species have changed from smaller to larger species in all the regions during 1940 to the early 1970's. The authors eventually found that the changes in species were accompanied by changes in the locations of spawning-nursery grounds from nearshore to offshore waters, which involves an important implication with key factors in the changes in species composition in connection with the hypothesis proposed by the authors.

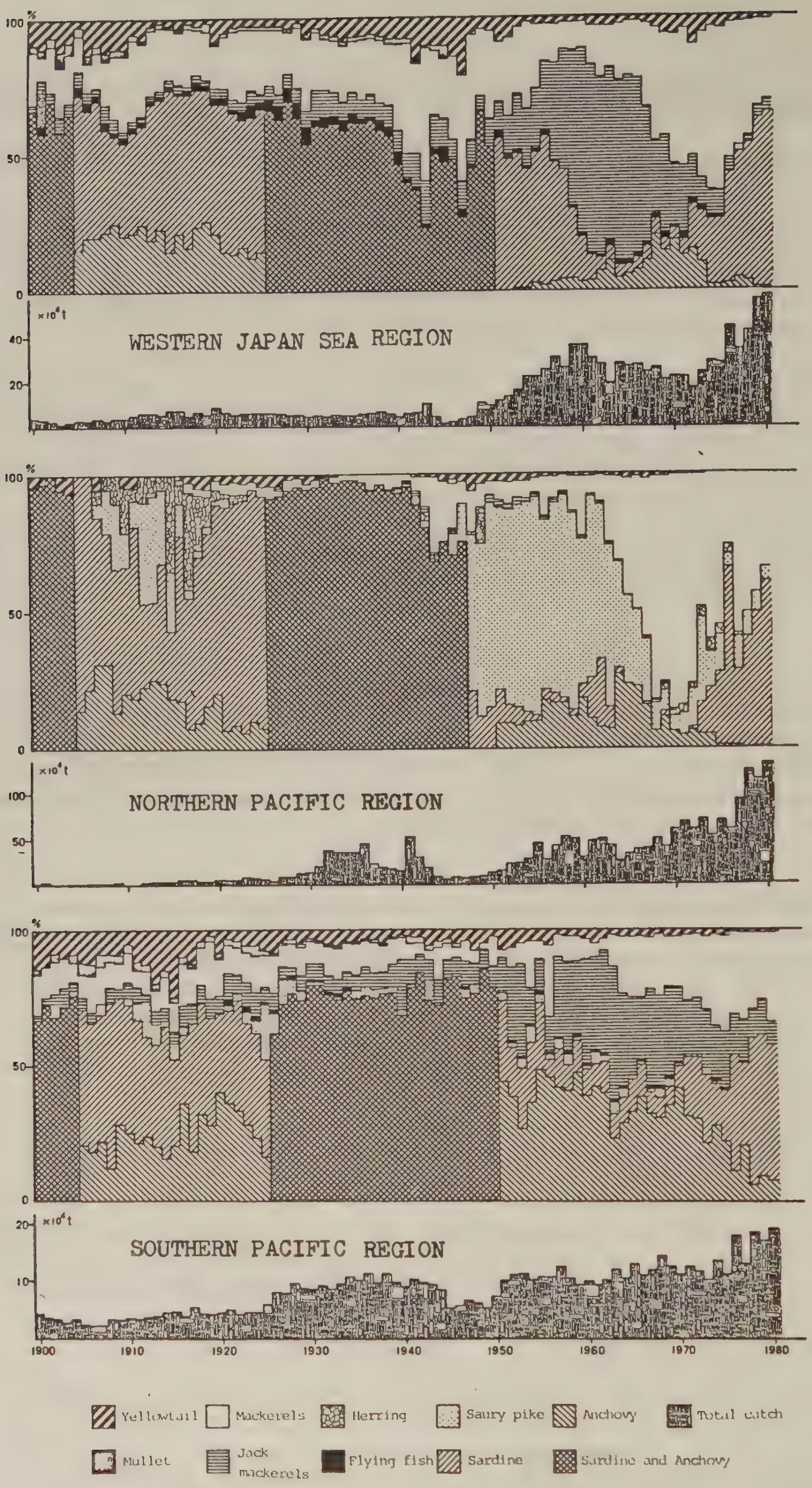
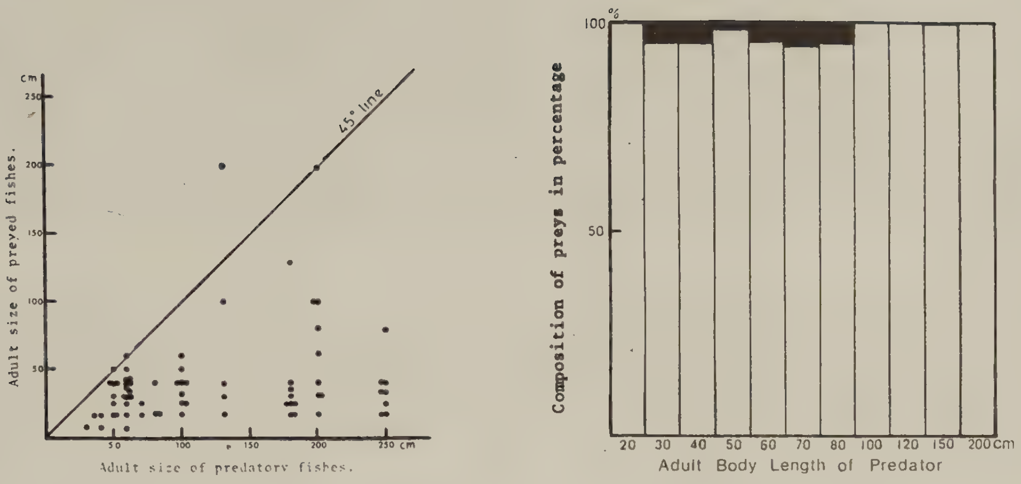


Figure 7

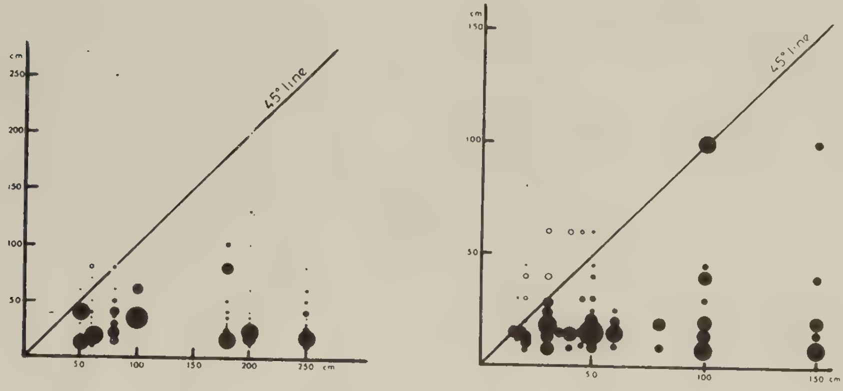
Historical change in the total catch and species composition of neritic pelagic fish around Japan by major sea region.



(a) From the general information.

(c) From the survey of stomach contents.

Blank part: preys smaller than predator
Shadowed part: preys larger than predator



(b) From the survey of stomach contents.

Figure 8

Comparison of body sizes between preys and predators. Data employed were cited from Hayashi et al., 1960, Kudo et al., 1969, Matsubara et al., 1965, Matsumiya 1980, Mikawa 1952, 1955, Misu 1964, Nishimura 1959, Okada 1970, Omori 1980, Saishu et al., 1965, Sato 1975, Toriyama 1958, Yamada et al., 1966, and Yokota et al., 1956, 1961.

The coastal species, such as sardine, are more advantageous than further offshore species to maintain the dominancy, in terms of nutrient condition, if nothing happens to them. If carnivorous plankton blooms in coastal waters simultaneously with the February to April spawning of coastal fish species, a massacre would occur of the larvae which would surely weaken year-class strength. At the same time, a substantial amount of feed plankton is produced as a result of the above-mentioned process. The authors assume that the species, which occupy adjacent areas and which have inherent potential to bloom could eventually colonize and become dominant in coastal areas. If the new species gains further strong reproductive power, it could gradually take over the entire range where the former dominant species prevailed. It should be noted that changes in species composition could have been initiated by the changes in year-class strength which declined in the former species and are reinforced in the new species. Such cyclic processes might occur repeatedly over several decade intervals, and the dominant species would have changed in turn.

The recent change in the dominance from mackerel to sardine may have followed a somewhat different process as both the body sizes and habitats of these two species are reverse from the above-mentioned general pattern. Mackerel is considered to be the outermost species among the abundant pelagic fish species along the Japanese coast and there were no further offshore species when mackerel dominated the coastal waters around Japan. The authors assume therefore that sardine took over the unoccupied area when mackerel stocks had declined due to extraordinarily large predatory loss of the larvae by the bursts of carnivorous plankton. The authors are unable, however, to say much about the inevitability of the burst of sardine, which is the most coastal species in the authors' categorization, compared to the other coastal species. A notable phenomenon was the observation that the change from mackerel to sardine took place throughout the coastal waters around Japan during nearly the same period.

It is interesting to note the fact that the species which have become dominant are limited to only a few species among many pelagic planktivores, though these are widely distributed around Japan. A typical exclusion is anchovy. The authors consider that the mobility and migratory nature of the selected species may have played a substantive role in the above-mentioned process. Indeed, mobile fish advantageously quickly take over the surplus area rather than less mobile species.

Sardine, currently dominating all Japanese waters, will likely be dominated by some other species some time later. The authors are unable to predict the next species to dominate as it is impossible to assume which species will be distributed in bordering offshore areas at the time of the next crisis for sardine larvae.

Supplementary analysis on carnivorous planktons

A comprehensive survey of plankton and fish larvae was carried out during 1965 to 1967 (Yamazi, 1971). Data on the distribution of the biomass of total zooplankton, carnivorous plankton and fish larvae collected during the survey is shown in Figure 9. The distribution pattern of carnivorous plankton shows a proportional trend to that of fish larvae which suggests the aggregative function of predatory plankton to the concentration of fish larvae.

Table 2 gives the annual change in the abundance of a typical carnivorous plankton, Chaetognatha in the southern coastal waters of Japan, where major spawning grounds of major planktivores are located, during Janaury to April every year when most of the spawning takes place. It is interesting to see that the timing of the three peaks of the abundance of Chaetognatha namely 1960, 1966-67 and 1972-73 coincide well with the periods when dramatic species change took place in the region, namely 1958-60, 1965-67 and 1973-75.

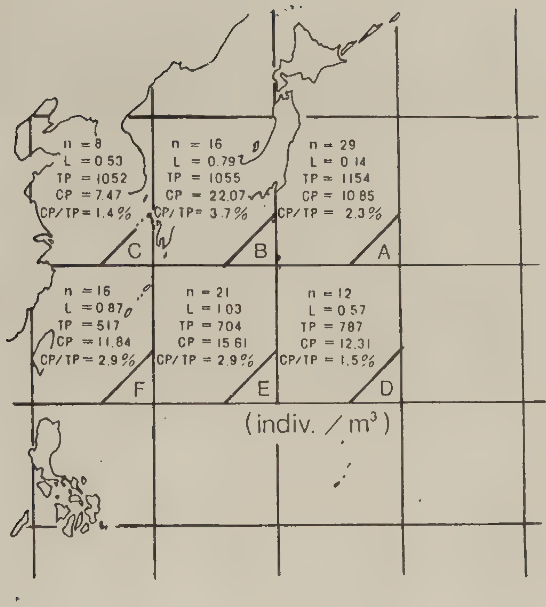


Figure 9

Comparison of the abundances among fish larvae, total zooplanktons and carnivorous planktons in the waters around Japan by 10-degree square area. The data were cited from Yamazi (1971) which were collected during February to May every year for 1965 to 1967.

n : number of observation, L : fish larvae,
TP : total zooplankton, CP : carnivorous plankton.

Another interesting phenomenon has been found in the oceanographic condition which may realize the burst or massive invasion of carnivorous plankton into the coastal waters. Kidachi (1982) reported that the abundance of Chaetognatha in spring along the southern coast of Honshu (mainland of Japan) is usually high when the Kuroshio current approaches the coast. The authors analyzed the data on the Kuroshio for 1960 to 1980 and found a trend in that the abundance of Chaetognatha (Table 2), increased when the axis of the Kuroshio tended to approach the coast and vice-versa. The finding implies that the change in dominancy of pelagic fish could possibly take place at nearly the same time along both the Pacific and Japan Sea coasts. It also suggests one possibility of predicting the occurrence of the next burst of carnivorous plankton in coastal waters and accordingly the change in species composition.

A NEW METHOD TO ASSESS THE STATE OF STOCKS ACCOMPANIED BY LARGE FLUCTUATIONS

Apart from the change in species composition, it is concluded that the assessment of stocks, which are usually accompanied by large fluctuations in abundance, is difficult using traditional methods. For instance, the catch of sardine exceeded 3 million tons in recent years but was less than 10,000 tons only 15 years ago and the traditional methods have been almost of no use for such a drastic change in abundance. It is now generally accepted among Japanese scientists that the sardine stocks will decline again some time in the future even if fishing ceases completely. The concept of the SY or MSY is not applicable to such stocks.

The authors think that a new management strategy should be established with a better biological basis and that the establishment of a certain level of abundance would be useful as a guidemark to manage the fisheries. The authors propose a new method for use in assessments of such stocks; the analysis of the age at maximum biomass of cohorts (Kawai, 1980).

Table 2. Annual change in the abundance of Chaetognatha, one of the typical carnivorous plankton, in the southern coastal waters of Japan during January to April every year.

Year	Total Number of Chaetognatha (inds.)	Average Number of Chaetognatha (inds./10 m^3)
1960	1 940	138.6
1961	1 710	61.1
1962	733	40.7
1963	1 104	50.2
1964	1 097	54.9
1965	1 316	50.6
1966	2 118	78.4
1967	1 908	61.5
1968	656	36.4
1969	282	40.3
1970	872	37.9
1971	293	32.6
1972	1 497	59.9
1973	790	60.8
1974	263	43.8
1975	241	34.4
1976	437	54.6
1977	417	46.3
1978	292	22.5
1979	689	53.0
1980	978	57.5

Mathematical expressions:

In the estimation of the age at maximum biomass of a cohort (t_s), the biomass of a year-class after the critical period (W_t) is given by

$$\begin{aligned} W_t &= w_t N_t \\ &= w_\infty (1 - e^{-kt})^3 N_0 e^{-Mt} \qquad \ldots.(8) \end{aligned}$$

where w_∞ denotes the maximum body weight and k growth coefficient. The age (t_s) at the maximum W_t is given under the condition of $dW/dt = 0$ as,

$$\frac{3ke^{-kt_s}}{1-e^{-kt_s}} - M = 0$$

hence

$$t_s = \frac{1}{k} \log \left(1 + \frac{3k}{M}\right) \qquad \text{....(9)}$$

The age (t_s) can therefore be determined by k and M. However, some modification of the function is better from the practical point of view as k and M usually are unstable conditions. Kawai (1970) reported that the growth coefficient (k) can be approximated from the age at first maturity (t_m) by

$$k = \frac{0.826}{t_m} \doteqdot \frac{5}{6} \cdot \frac{1}{t_m}$$

Tanaka (1960) proposed the approximation of the relationship between M and lifespan (t) to be

$$M = \frac{2.5}{t_\lambda} = \frac{5}{2} \cdot \frac{1}{t_\lambda}$$

substituting these relations into equation (9), t_s is now given as

$$t_s = \frac{6}{5} t_m \log \left(1 + \frac{t_\lambda}{t_m}\right) \qquad \text{....(10)}$$

The age at maximum biomass can, therefore, be estimated from the age at first maturity (t_m) and lifespan (t_λ).

It was ascertained, after the investigation of about 30 marine fish species, that there is a general rule that

$$t_s > t_m$$

which may be a rationale in reproductive potential maintenance.

More importantly, the distribution of t_s is concentrated in a zone around $^1/3$ of the interval between t and t_m as is shown in Figure 10. On average the relationship is given as

$$t_s = t_m + \frac{1}{3} (t_\lambda - t_m)$$

It is surprising to find that the relationship is commonly observed, irrespective of fish species (variation of t_λ and t_m) which may be derived from the close relationship among the three ages and their potential effects throughout fish species.

When the mortality coefficient is increased/decreased by a difference, α, the age at maximum biomass changes to (t_s') as

$$t_s' = \frac{1}{k} \log \left(1 + \frac{3k}{M + \alpha}\right) \qquad \text{....(11)}$$

The difference between t_s and t_s' is

$$t_s - t_s' = \frac{1}{k} \log \left(1 + \frac{3\alpha k}{M(M + \alpha + 3k)}\right) \qquad \text{....(12)}$$

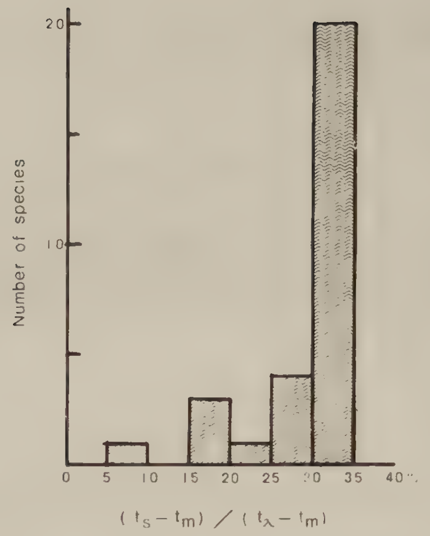


Figure 10

Frequency distribution of the number of species against the relative position of the age at maximum biomass (t_s) over the ages at first maturity (t_m) and lifespan (t_λ).

that is

$$\alpha > 0, \quad t_s' < t_s$$

and

$$\alpha < 0, \quad t_s' > t_s$$

In other words, the age at maximum biomass decreases in accordance with the increase in mortality. If mortality is seriously increased, t_s approaches rapidly to t_m and would even surpass it in an extreme case which is considered to be a badly deteriorative condition for the cohort for future reproduction.

The condition under which $t_s = t_m$ are given from

$$\frac{1}{k} \log \left(1 + \frac{3k}{M + \alpha}\right) = t_m$$

hence

$$\frac{\alpha}{M} = 0.769 \left(\frac{t_\lambda}{t_m}\right) - 1 \qquad \text{....(13)}$$

The average value of t_λ/t_m for the 30 species examined is 2.626, putting this into equation (13).

$$\alpha = 1.018 \text{ M}$$

which indicates that the age at maximum biomass decreases equivalent to the age at first maturity when the mortality coefficient is increased to about double, for any reasons, of the usual value under stable natural conditions.

APPLICATION TO SARDINE STOCKS AROUND JAPAN

As was discussed, the age at maximum biomass (t_s) is much larger (older) than the age at first maturity (t_m) when the stocks are under normal conditions and decreases when the stocks decline for any reason. Observation of the value of t_s and changes in comparison to t_m in a given stock, is therefore a good measure to assess the state of the stock. The time series data on the relative position of t_s could give us the magnitude of the changes occurring. It should be noted here that the increase in mortality is not necessarily defined/limited to specific origins. Whatsoever causes the loss of a cohort, natural or artificial, should be taken into account as the factor on changing the position of t_s. Figure 11 shows an example of the preliminary application of the new method to the sardine stock around Japan. The value of t_s (= 4.0) denoted in the figure indicates the value estimated by equation (10) in the previous section, which is the value under the normal condition of the stock being determined by t_m and t_λ, while the observed value (t_s') for each of the year-classes is shown by the abscissae of the peaks on age compositions in weight.

It is apparent that t_s' was far below (younger) than t_m during the poor catch period, (year-classes 1948-50) which indicates seriously deteriorated status of the reproductive potential of the stock. It, however, is larger again when the stock abundance began to recover after the early 1970's and is equivalent to or even surpasses the value of t_m in recent year-classes (1975-77 in a favourable catch period) which clearly shows the stable and quite favourable status of the stock. The authors believe this type of analysis would be one of the useful methods when it is established through further studies to clarify the problems on both the theoretical and practical aspects (data collection etc.).

DISCUSSION

Apart from the discussions on the technical aspects of the proposed hypotheses specified at the end of each section, the authors intend to present here some considerations from a broader perspective.

Comparative analysis with demersal fish stocks

Drastic changes in species composition in demersal fish stocks has rarely been observed. In some boreal areas a single species sometimes predominates over the other species, e.g. Alaska pollack in the eastern Bering Sea and Okhotsk Sea, but its dominancy has not changed. In temperate areas, on the other hand, no single dominant species overwhelms the other and changes in species composition usually take place in gradual and moderate progression. The authors assume that these phenomena would have derived from the nature of larval mortality of those species.

Demersal fish are generally omnivores which feed on a variety of organisms such as plankton, benthos, fish, molluscs, crustacea etc. The authors consider that the mechanisms and processes of larval mortality for demersal fish are much more diverse than those of planktivores and piscivores which are placed at the extreme - both ends of the feeding habit of fish. In other words, the fish located at the intermediate position of feeding habit might have attained the diversity in larval mortality for which the extreme functions such as cannibalism and predation by carnivorous planktons are not general.

On the other hand, the rapid and drastic changes in abundances of planktivores would not have taken place if some density-independent impact did not affect the larvae during their critical stage. The abundance of piscivores would have been comparatively stable in this regard, density-dependent loss during the critical stage, and changes in dominance have rarely been observed. The diversity of larval mortality of demersal fish might also be one of the major reasons preventing drastic changes in abundance or species composition.

Another feature of demersal fish is that often demersal fish groups are rich in species as a community. It is imaginable that such variety would have also functioned to prevent the drastic changes at both the species and community levels. Figure 12 shows an example of a very stable status of year-class strengths of branquillos taken from Japanese waters, from the same criterion as given in Figure 11 in regard to t_s, t_s' and t_m. The species composition of the catch also shows a stable trend. The authors assume that the "Diversity-Stability Rule", which is commonly applied to terrestrial ecological studies, would also be applicable to marine teleosts.

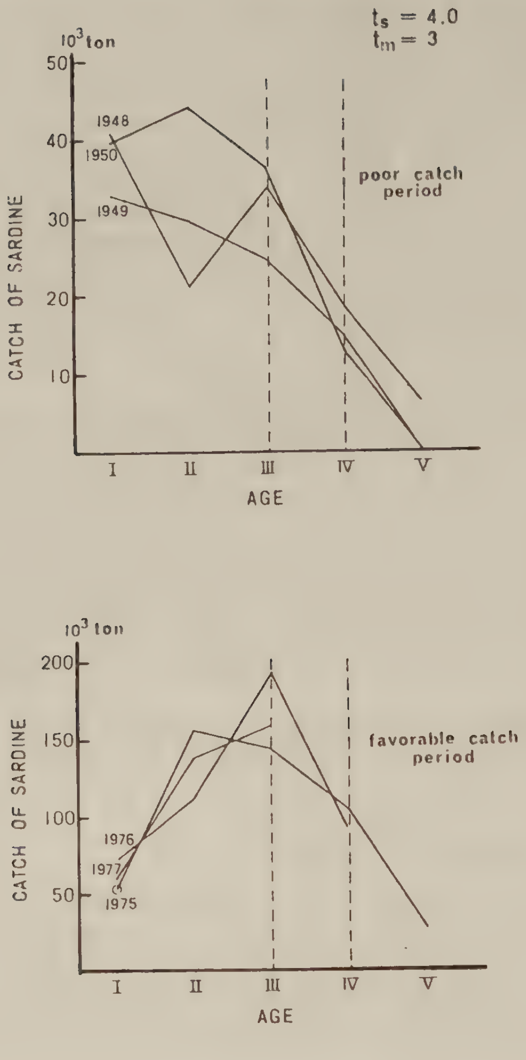


Figure 11

Change in the age composition in weight of the selected year-classes of Japanese sardine in comparison with the ages at first maturity (t_m) and at maximum biomass (t_s). The value of $t_s = 4.0$ denoted in the figure was estimated by equation (10) in the text which was determined by t_m and t_λ under the normal condition of the stock, while the observed value of the age at maximum biomass (t_s') for each year-class is shown by the abscissa of the peak of each age composition figure.

Change in dominance on a world-wide scale

The authors analyzed the changes in dominance observed in many productive waters in the world from a comparative basis, in which the diversity index was applied to the species composition in each of the FAO Fishing Areas (Kawai et al., 1983). The authors found that diversification has occurred in many areas since 1965 and an area, where a reverse trend was shown, was scarcely found. Secondly, two major zones of the world oceans were identified, namely the Western Pacific and the Eastern Atlantic, which were considered to have experienced similar phenomena in changes in the prominent species biomass there, and subsequent dramatic changes in species composition occurred. The authors assume that these phenomena and the long-term trends in these are similar in nature even though they are separate, independent processes, with different species, timing and magnitudes. It is

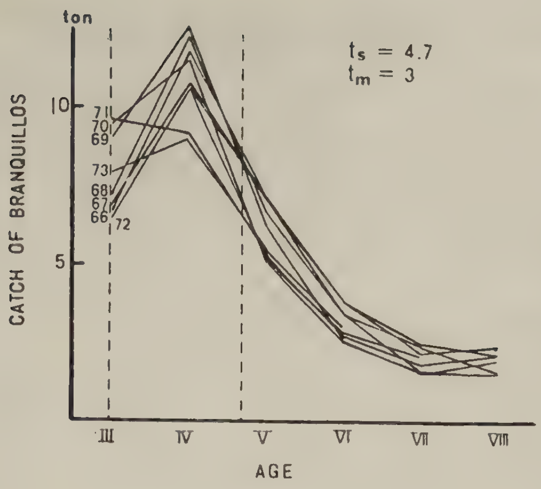


Figure 12

Change in the age composition in weight of branquillos for the year-classes 1966-72 caught along the Japanese coast. See the notes in Figure 11 for the notation and interpretation.

therefore concluded that the principles involved result from usual evolutionary processes in marine teleosts, and that the changes in species composition would be a typical characteristic of neritic pelagic fish resources.

It is also hypothesized that if drastic changes in dominance are mostly due to carnivorous plankton in connection with the change in the oceanographic conditions, and if such conditions are cyclically-realized on a global basis, there would be a firm rationale for the coincidence of such phenomenon on a world-wide scale.

Future studies

The authors have identified the following issues needing to be taken into account in order to validate the proposed hypotheses and in order to eventually develop methods to be applied to stock assessment of neritic pelagic fish resources for management purposes.

(1) Consideration of the evolutionary aspects of fish should be more intensively incorporated into all studies. It is the authors' view that the dramatic changes in species composition will take place repeatedly in the future and any direct measure to control them will not be applicable in the immediate future. Clarification of their nature, principles and roles are, therefore, considered to be of basic importance.

(2) More observation and analysis should be carried out specifically on the interspecific relationships among fish and plankton.

(3) Comparative studies of the phenomena observed in different areas should be intensified. There is no doubt that such studies would improve understanding of both local and general processes, as well as the differences in species, biological and environmental conditions resulting from such processes.

Appendix 1 Important biological features of the major 75 species of Teleostei occurring in the waters around Japan.

Japanese Name	Scientific Name	Body Length in Adult (cm)	Diameter of Egg (mm) 0-Isolated Floating X-Adhesive	Body Length at Hatch Out (mm)	Body Length at 1 Age (cm)	Biological Minimum Size (cm)	Number of Days to Hatch Out
Tatunootosigo	*Hippocampus coronatus*	8		9.0	8		
Siwaikanago	*Hypoptychus dybowskii*	9	1.8 X				7
Kibinago	*Spratelloides japonicus*	10	1.2 X	4.6			7
Katakuchiiwashi	*Engraulis japonica*	15	1.1 0	2.6	11	8	1.3
Sappa	*Harengula zunasi*	15					
Nigisu	*Glossanodon semifasciatus*	20	1.5				
Kurumesayori	*Hemiramphus kurumeus*	20	1.4				
Mahaze	*Acanthogobius flavimanus*	25	0.8 X				28
Ariaketobiuo	*Cypselurus starksi*	25	1.7 X	5.2	25	25	18
Yōziuo	*Syngnathus schlegeli*	25		9.5		21	
Ikanago	*Ammodytes personatus*	25	0.7 X	4.0	10		9
Maiwasi	*Sardinops melanosticta*	25	1.4 0		16	15	2.5
Mebaru	*Sebastes inermis*	25			9	16	
Kasago	*Sebastiscus marmoratus*	25			7		
Konosiro	*Konosirus punctatus*	25	1.5 0	3.3	15	15	2
Kawahagi	*Stephanolepis cirrhifer*	25	0.7 X	2.0			2.5
Umitanago	*Ditrema temmincki*	30			12		
Hosotobi	*Cypselurus opisthopus hiraii*	30	1.6 X	4.8			10
Hatahata	*Arctoscopus japonicus*	30	2.0 X	9.0	7	16	50
Urumeiwasi	*Etrumeus micropus*	30	1.3 0	3.8	14		
Kitizi	*Sebastolobus macrochir*	30	1.2 0	2.6	9	17	9
Ibodai	*Psenopsis anomala*	30					
Sanma	*Cololabis saira*	35	1.6 X	7.3	20		13
Sayori	*Hemiramphus sajori*	35	2.2 X	7.2	20	25	14
Ainame	*Hexagrammos otakii*	35	2.1 X	7.4	15	19	25
Kidai	*Dentex tumifrons*	35	0.9 0	1.7	15		1.7
Tukusitobiuo	*Cypselurus heterurus döderleini*	35	2.0 X	5.6	20	20	13
Tobiuo	*Prognichthys agoo*	35	1.5 X	4.9			11
Nisin	*Clupea pallasi*	40	1.5 X	7.2	15	22	25
Tidai	*Evynnis japonica*	40	1.0 0	2.1	11		
Inunosita	*Cynoglossus robustus*	40	0.9 0	1.8	14	23	0.7
Gisu	*Pterothrissus gissu*	40			16		
Tokageeso	*Saurida elongata*	40					
Kinguti	*Pseudosciaena manchurica*	40	1.5 0	3.4	8	20	2.5
Gomasaba	*Scomber tapeinocephalus*	40			28		
Komai	*Eleginus gracilis*	40	0.9 X	2.5	20	25	5.5
Isaki	*Parapristipoma trilineatum*	40	0.9 0	1.6	13		1.2
Maazi	*Trachurus japonicus*	40	0.9	2.5	11	20	1.7
Akagarei	*Hippoglossoides dubius*	40	1.4		13	30	
Souhatigarei	*Cleisthenes herzensteini*	40	0.9 0	3.0	8	18	3.3
Babagarei	*Microstomus achne*	40	1.8 0	4.3	10		11
Hōbō	*Chelidonichthys spinosus*	40	1.2 0	3.2	12	27	4.2
Maeso	*Saurida undosquamis*	45			11		
Kuroguti	*Argyrosomus nibe*	45	0.9		11	25	
Mezina	*Girella punctata*	50	1.0 0	2.3	11		2.5
Hamatobiuo	*Cypselurus pinnatibarbatus japonicus*	50	2.0 X	5.2			13
Kurodai	*Acanthopagrus schlegeli*	50	0.9	2.0	12	19	1.7
Hokke	*Pleurogrammus azonus*	50	2.5 X	10.0	21		65
Marusooda	*Auxis tapeinosoma*	50	1.0	2.7	25	27	
Siroguti	*Argyrosomus argentatus*	50	0.8 0	1.5	15	20	0.9
Akaamadai	*Branchiostegus japonicus japonicus*	50	1.0		15	13	
Masaba	*Scomber japonicus*	50	1.1 0	3.0	25	26	2
Isidai	*Oplegnathus fasciatus*	55	0.9 0	2.2			1.5
Hira	*Ilisha elongata*	60	2.4 0	5.1			1.3
Suketodara	*Theragra chalcogramma*	60	1.5 0	3.9	15	34	13
Bora	*Mugil cephalus*	60	1.0		20	40	
Torahugu	*Fugu rubripes*	70	1.3 X	2.7	25		10
Wanieso	*Saurida tumbil*	65	1.2		18	35	
Suzuki	*Lateolabrax japonicus*	80	1.3 0	4.5	20		4.5
Hirame	*Paralichthys olivaceus*	80	0.8 0	1.7	17	48	2.3
Madai	*Pagrus major*	100	1.2 0	2.3	12	36	2.3
Datu	*Ablennes anastomella*	100	3.3 X	12.6	47	40	13
Sabahi	*Chanos chanos*	100	1.2 0			100	
Menada	*Liza haematocheila*	100					
Tenzikudatu	*Tylosurus melanotus*	100	3.4 X	10.0			11
Katuo	*Katsuwonus pelamis*	120			16		
Buri	*Seriola quinqueradiata*	120	1.2 0	3.5	40	69	2
Madara	*Gadus macrocephalus*	120	1.1 X	3.9		60	17
Binnaga	*Thunnus alalunga*	120	0.6 0		30	87	
Siira	*Coryphaena hippurus*	180	1.5 0	4.0		70	2
Kihada	*Thunnus albacares*	200	1.0 0		51	110	
Mebati	*Thunnus obesus*	200	0.6 0	1.5	55	100	0.9
Kuromaguro	*Thunnus thynnus*	250	0.8				
Ohyo	*Hippoglossus stenolepis*	270	3.3	11.2	8		

..//

APPENDIX CONTINUED

Order of Species C : Clupeida P : Percida Pl : Pleuronectida B : Belonida Co: Cottida	Living Condition P:Pelagic D:Demersal I:Intermediate	Food Zp:Zooplankton Vp:Vegetable plankton F :Fish B:Bottom Eater 0 :Others	Egg Condition 0-Isolated Floating X-Adhesive	Fecundity (x 10' Eggs)	Number of Oil Globules m:Plural	Number of days to Hatch Out	Life-Span (Year)	First Adult Age (Year)	Number of Centrums	Type of Stomach	Number of Gill-Rakers	Type of Dorsal Fins 0-Soft P:Spinous	Number of Scales on Lateral Line
		0, F					1					0	
	I	Zp	X	0.01	m	7			56			0	
C	I	Zp	X		m	7				Y		0	42
C	P	Vp, Zp	0	0.2	0	1.3	2.5	1		Y		0	42
	I	Vp, Zp							45		73	0	42
C	D	Zp, F, B		0.6	1		3	1			37	0	51
	I	Vp, Zp							51	0		0	80
	I	B, Vp	X	1.9		28	1.5	1				P	58
B	P	Zp	X	0.8		8		1	11	0	33	0	33
				0.1								0	
	I	0	X	0.4	1~2	9	3	1	63			0	
C	P	Vp	0	1.5	1	2.5	6	3		Y		0	45
Co	D	Zp		4.5			6	3	26	*		P	
Co	D	Zp		10			7	2	25	*	22	P	
C	I	Vp, Zp	0	22	1	2	7	1		U		0	50
	D	Zp	X	15	m	2.5			19	1		P	
		0						1					
B	P		X	0.7		10		1	46		28	0	33
P	D	Zp	X	0.2		50			49	*		P	
C	P	Zp	0		0		5			Y		0	55
Co	D	B, 0			1	9			29		20	P	
	D	0								*		P	55
B	P	Zp	X	0.5	m	13	4	3	61	0		0	100
B	I	Vp, Zp	X	0.3	m	14	2.5	2	61	0		0	100
Co	D	Zp, F, B	X	0.4	m	25	5	2		Y		P	
P	D	Zp, E, B	0	2.5	1	1.7		3.5		V	19	P	48
B	P		X	1.3		13		1	47		23	0	33
B	P	Zp	X	1.5		11			47	0		0	35
C	P	Zp	X	6.5	0	25	18	4		Y		0	52
P	D	B, 0	0		1	2	10				20	P	58
Pl	D	B	0		m	0.5		3	62			0	68
C	D											0	112
	D			8.4					63			0	65
P	D	Zp	0	6.5	1	2.5	5	2	29			P	55
P	P	F, Zp				3	4	1				P	
	D	0	X	11.8	m	5.5	7	2.5				0	157
P	I		0	55.5	1	1.2	5				42	P	111
P	P	F, Zp	0	26	1	1.7	6			*		P	71
Pl	D	Zp, F, 0		17			10					0	93
Pl	D	Zp	0	70		3.3	9	3	39			0	83
Pl	D	B	0	34		11	10		48			0	110
Co	I	B, F	0		1	4.2		4				P	180
	D	F							49	*		0	51
	D			7.5	1		7	3				0	52
P	I	0	0		1	2.5				*		P	53
B	P	Zp	X	2.1	0	13			51	0	20	0	43
P	D	B, Zp	0		1	1.7		3		V	16	P	52
Co	D	F, B, 0	X	25.5	m	65	8	3	60			P	162
P	P				1			2			46		
P	D		0	35	1	0.9	7	3				0	48
	D	B, F, 0								1		P	72
P	P	Zp, F	0	75	1	2	6	2	31	*		P	215
	D	Zp	0		1	1.5				V		P	98
C	I	F, B	0		1	1.3						0	53
	D	F	0	63	6	13	10	4.5	51	*		0	
	I			220	1		6	4			80	P	40
	I	F	X	108	m	10			22			0	
	D	F		36			7		53			0	58
P	I	0	0	19.5	1	4.5	7	2.5	36		25	P	
Pl	D	0, F	0	30	1	2.3	10	3	37	*	23	0	114
P	D	F, B, 0	0		1	2.3	20			V	17	P	56
B	I	F	X	0.5		13	4	1		0		0	
C	D		0	450	0								
		0, Vp										P	37
B	I		X			11						0	
P	P	F	0					4	21	*	53	P	
P	P	F	0	110	1	2	7	3		*	30	P	215
	D	F	X	325		17	10	4	54	*		0	295
P	P	F	0	195			9	6			29	P	
P	P	F	0	395	1	2			31	*		0	295
P	P	F	0	300			8			*	31	P	
P	P	F	0	450	1	0.9	7	3		*	27	P	
P	P	F	0	100	1		15	3		*	35	P	
Pl	D	F		200	0			9	51			0	168

* V-Shape in Reverse

REFERENCES

Asami, T. et al. 1967. Studies on the features of yellowtail in spawning and larval period and on the tagging experiments in its juvenile stage. Kenkyu Seika, published by the Agriculture, Forestry and Fisheries Research Council, Tokyo, Japanese Government. 30:1-61.

Fraser, J.H. 1969. Experimental feeding of some Medusae and Chaetognaths. J.Fish.Res.Bd.Canada. 26:1743-1762.

Hamada, H. 1965. Study on relation of food between Sagitta crassa and Ammodytes personatus. Bull.Hyogo Pref.Fish.Exp.St. 3:1-6.

Hattori, S. 1962. Predatory activity of Noctiluca on anchovy eggs. Bull.Tokai Reg.Fish.Res.Lab. 9:211-220.

Hayashi. T. and Y. Yamaguchi. 1960. Study on food niches of the benthic piscivors. Kenkyu Seika, published by the Agriculture, Forestry and Fisheries Research Council, Tokyo, Japanese Government. 2:1-113.

Ichimura, T. 1978. Culture fisheries at the phase of turning point in circumstances. Suisan Shinko. 127:1-21.

Isibasi, K. 1981. Changes of neritic pelagic fish resources around the world. I. Sakana, published by the Tokai Regional Fisheries Research Laboratory. 27:25-34.

Kawai, T.A. 1970. A review and some discussions on growth equation. Bull.Jap.Soc.Sci.Fish. 36(3):289-296.

____________. 1978a. A study of comparative biology on Japanese pisces to population analysis. I. The statistical analysis on the growth of fishes. Bull.Tokai Reg.Fish.Res.Lab. 93:29-43.

____________. 1978b. A study of comparative biology on Japanese pisces to population analysis. II. The statistical analysis on the feeding habits of fishes. Bull.Tokai Reg.Fish.Res.Lab. 96:75-92.

____________. 1979. On the effects of feeding habits of fishes to the fluctuation of fish resources. Rep.Fish.Res.Invest.Japan Gov. pp. 71-84. In Divisional report of demersal fisheries in western region of Japan.

____________. 1980. A study of comparative biology on Japanese pisces to population analysis. IV. The quantitative analysis on biological production of a cohort. Bull.Tokai Reg.Fish.Res.Lab. 103:31-40.

Kawai, T. and K. Isibasi. 1979. A study of comparative biology of Japanese pisces to population analysis. III. A quantitative analysis on the larval mortality by cannibalism. Bull.Tokai Reg.Fish.Res.Lab. 100:79-89.

____________. 1981. A study of comparative biology on Japanese pisces to population analysis. V. A quantitative analysis on larval mortality devoured by carnivorous plankton. Bull.Tokai Reg.Fish.Res.Lab. 104:55-66.

Kawai, T., K. Isabasi and T. Takahashi. 1983. Changes of neritic pelagic fish resources around the world. II. Sakana. (29) (in press).

Kidachi, T. 1982. On the distribution of macro-plankton in coastal region and Kuroshio. Bull.Coast.Ocean. 19(2):131-148.

Kudo, S. et al. 1969. Food study of bottom fish in continental slope of Tosa-Wan. Bull.Nansei Reg.Fish.Res.Lab. 2:85-103.

Lebour, M.V. 1923. The food of plankton organisms. J.Mar.Biol.Assoc.U.K. 13:70-92.

Lillelund, K. and R. Lasker. 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish.Bull. 69(3):655-667.

Matsubara, K. and A. Ochiami. 1965. Ichthyology (Part II). Tokyo, Koseisha-Koseikaku Co. Ltd. 958 p.

Matsumiya, Y. 1980. Stomach contents examination of the piscivorous demersal fishes in Shijiki Bay. Bull.Seikai Reg.Fish.Res.Lab. 54:333-342.

Mikawa, M. 1952. Studies on the digestive system and feeding habit of bottom fishes in the north-eastern sea area along the Pacific coast of Japan. Bull.Tohoku Reg.Fish.Res.Lab. 1:20-24.

____________. 1955. Studies on the digestive system and feeding habit of bottom fishes in the north-eastern sea area along the Pacific coast of Japan. III. Atheresthes evermanni Jordan et Starks. Bull.Tohoku Reg.Fish.Res.Lab. 4:136-146.

Misu, H. 1964. Fisheries biology on the ribbon fish (Trichiurus lepturus Linne) in the East China Sea and the Yellow Sea. Bull.Seikai Reg.Fish.Res.Lab. 32:1-57.

Nishimura, S. 1959. Foods and feeding habit of the Pacific mackerel in the coastal waters of Niigata Prefecture, Japan Sea in 1958. Ann.Rep.Nihonkai Reg.Fish.Res.Lab. 5:77-87.

Okada, K. 1965. Illustrated encyclopaedia of the fauna of Japan. Tokyo. The Hokuryukan Co. Ltd. 763 p.

____________. 1970. Some observations on the feeding activity of the sharp toothed eel Muraenesox cinereus (Forskal) in the East China Sea. Bull.Seikai Reg.Fish.Res.Lab. 38:131-146.

Omori. M. 1980. Feeding habit of yearling red sea bream (Pagrus major) in Yuya Bay. Bull.Seikai Reg.Fish.Res.Lab. 54:93-109.

Saishu, K. et al. 1965. On feeding habit of Gurnaid Chelidonichthys spinousus (McClelland) in the East China Sea and the Yellow Sea. Bull.Seikai Reg.Fish.Res.Lab. 33:47-59.

Sato, Y. 1975. Studies on the life history of the bastard halibut Paralichthys olivaceus (Temmink et Schlegel) near Sendai Bay. Bull.Tohoku Reg.Fish.Res.Lab. 35:15-30.

Shirota. A. 1975. Fresh-marine organisms as living feed for fishes. Tokyo, Koseisha-Koseikaku. 514 p.

____________. 1978. Studies on the mouth size of fish larvae. II. Specific characteristics of the upper jaw length. Bull.Jap.Soc.Sci.Fish. 44(11):1171-1177.

Suehiro, Y. 1941. A study on the digestive system and feeding habits of fish. Jour.Zool. 10(1):1-301.

Tanaka, S. 1960. Studies on the dynamics and the management of fish populations. Bull.Tokai Reg.Fish.Res.Lab. 28:1-200.

Toriyama. M. 1958. On diurnal rhythm in the feeding activity of Saurida undosquamis (Richardson) and Upeneus bensasi (Temminck et Schlegel). Rep.Nankai Reg.Fish.Res.Lab. 9:84-91.

Uchida, K. (ed.). 1958. Studies on the eggs, larvae and juveniles of Japanese fishes. Series I. Fukuoka, Japan. Second laboratory of fisheries biology, Fisheries Department, Faculty of Agriculture, Kyushu University, 187 p.

Yamada, U., M. Tagawa and H. Mako. 1966. On the feeding activity of lizard fish Saurida tumbil in the East China Sea. Bull.Seikai Reg.Fish.Res.Lab. 34:11-25.

Yamazi, I. 1971. Data report and distributional maps of the CSK standard zooplankton samples. Misc.Reps.Nat.Sci.Museum. 6:1-703.

Yokota. T. et al. 1956. On the fish community in the view of feeding habit. Rep.Nankai Reg.Fish.Res.Lab. 3:73-83.

____________. 1961. Studies on the feeding habit of fishes. Rep.Nankai Reg.Fish.Res.Lab. 14:1-234.

VARIATIONS IN PARENT STOCK AND RECRUITMENT OF PILCHARD AND ANCHOVY POPULATION IN THE SOUTHERN BENGUELA SYSTEM

by

Peter A. Shelton and Michael J. Armstrong

Sea Fisheries Research Institute
Private Bag X2
Rogge Bay 8012
Cape Town
South Africa

Resumen

La dispersión de los puntos observados en stocks de Clupeoides frecuentemente hace que la elección de la curva de reclutamiento sea dífícil y arbitraria. El efecto dominante del componente aleatorio (independiente de la densidad) enmascara la relativamente debíl respuesta regulatoria de la población. Si las respuestas regulatorias son ingnoradas completamente, la asesoría para la ordenación a medio tiempo de especies de vida corta debe basarse en información obtenida y de censos de pre-reclutas hechos inmdiatamente antes de que se inicie la actividad de pesca sobre esa clase anual en partícular. Es dudoso que en Sudáfrica se pueda interrumpir o reducir el esfuerzo de pesca en breve tiempo si se detecta una clase anual pobre. Una estrategia alternativa es elegir una curva de reclutamiento que se ajuste mejor, y usar la medida de los residuos para determinar la probalidad de diferentes rendimientos a varios niveles de mortalidad por pesca. Un enfoque de ese tipo se beneficiará de un entendimiento de cómo los mecanismos compensatorios potenciales pueden influir, aunque sea débilmente, en la forma de la curva de reclutamiento. Hay una lista interminable de posibles estrategias compensatorias que pueden ser puestas en evidencia por una población de peces pelágicos. En la sardina de Sudáfrica (*Sardinops ocellata*) y anchoveta (*Engraulis capensis*) hay evidencias de que la edad de la madurez y el peso promedio de las gónadas pueden tener un efecto regulador importante. La geografía del desove así como el comportamiento del cardúmenaje y la distribución, que se evidencian por la capturabilidad, pueden también afectar la forma de las curvas de reclutamiento. La consecuencia general de una respuesta compensatoria es la de mantener el reclutamiento por encima de la línea del remplazamiento cuando se plotea el stock y los reclutas, y permitir que se pueda obtener un rendimiento relativamente alto a niveles de biomasa bajos. Si se permite que la captura exceda la capacidad de compensación de la población, entonces el colapso será rápido siguiendo la pendiente de la parte izquierda de la curva de reclutamiento. Cuando se para la explotación, los mecanismos depensatorios por debajo del nivel de la línea del remplazamiento pueden evitar que la población se recupere inmediatamente. El incremento de la presión predatoria debido a una división de los cardúmenes, agregada a un cambio en el mecanismo de predación a un nivel poblacional menor, que pueden conducir a la creación de un segundo nivel de equilibrio. El hecho de que la biomasa de la sardina Sudáfricana se haya estabilizado a un nivel de biomasa reducido después de su gran caída en los años 1960s, a pesar del hecho que el esfuerzo es dirigido hacia la captura de esta especie para enlatado, puede ser una evidencia circunstancial de un segundo equilibrio.

INTRODUCTION

In clupeoid stocks the observed scatter of point often makes the choice of a recruitment curve difficult and arbitrary. The dominant effect of the variable density-independent component masks the relatively weak population regulatory responses. It has been estimated by MacCall (1980) that in *Engraulis mordax* the density-dependent coefficient in recruitment is only one-tenth the density-independent coefficient.

If the weak, underlying population regulatory response is ignored entirely then medium-term management of short-lived species must give way to information gained from a prerecruit census immediately prior to the start of fishing activity on the particular year class. In the South African context it is doubtful whether fishing effort could be sufficiently reduced at short notice if a weak year class were detected. The alternative strategy is to choose a recruitment curve that gives the best fit and to use the variance of the residuals to determine the probability of different yields at various levels of fishing mortality. Such an approach would benefit from an understanding of how potential compensatory mechanisms could influence, albeit weakly, the shape of the recruitment curve.

There is an open-ended list of possible compensatory strategies that may be displayed by a pelagic fish population. Recently MacCall (1980) and Csirke (1980) have shown that cannibalism of eggs by adults is one of the important mechanisms regulating the abundance of *Engraulis mordax* off California and *Engraulis ringens* off Peru. In the South African pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* there is evidence that age at maturity and mean gonad weight may have important regulatory consequences. In addition, spawning geography as well as schooling behaviour and distribution as evidenced by catchability may also effect the shape of the recruitment curve.

STOCK SIZE AND RECRUITMENT TRENDS

The pilchard population rose to a biomass peak in 1959 of over 2 000 000 tons (Virtual Population Analysis estimate, m = 0,5) yielding a maximum catch of 410 000 tons in 1962. Spawner biomass peaked at just over 600 000 tons in 1961 (Figure 1). The stock subsequently declined rapidly to less than 300 000 tons by 1966. Total biomass has currently stabilized at around 200 000 tons and spawner biomass at less than 100 000 tons despite the fact that effort is directed towards catching this species for canning. With a change to a small mesh net during 1964 and 1965 the anchovy has made an increasing contribution to the fishery (Newman and Crawford 1980) and current annual catches are about 300 000 tons. Virtual Population Analysis (VPA) estimates indicate a biomass increase in this species due to good recruitment in 1973 (Figure 2) although the fishery is still dependent on catches of fish one year old and less. A comparison shows that peak pilchard spawning biomass was substantially larger than the current anchovy spawning biomass (Figure 1) but that anchovy recruitment has in nearly all instances been larger and has displayed fluctuations that are less damped (Figure 2), in keeping with rapid maturity and a short generation time.

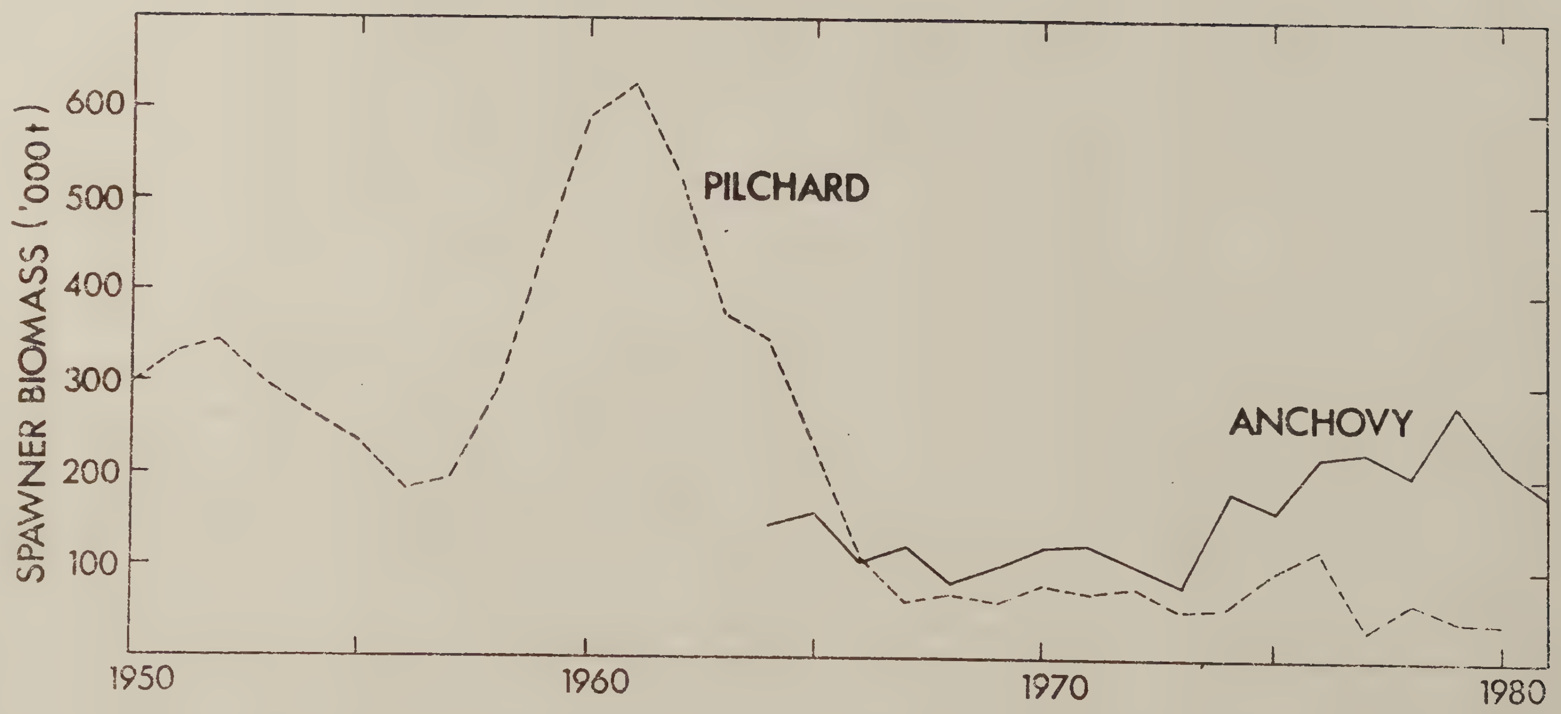


Figure 1. Time series of South African pilchard and anchovy spawner biomasses from VPA analysis.

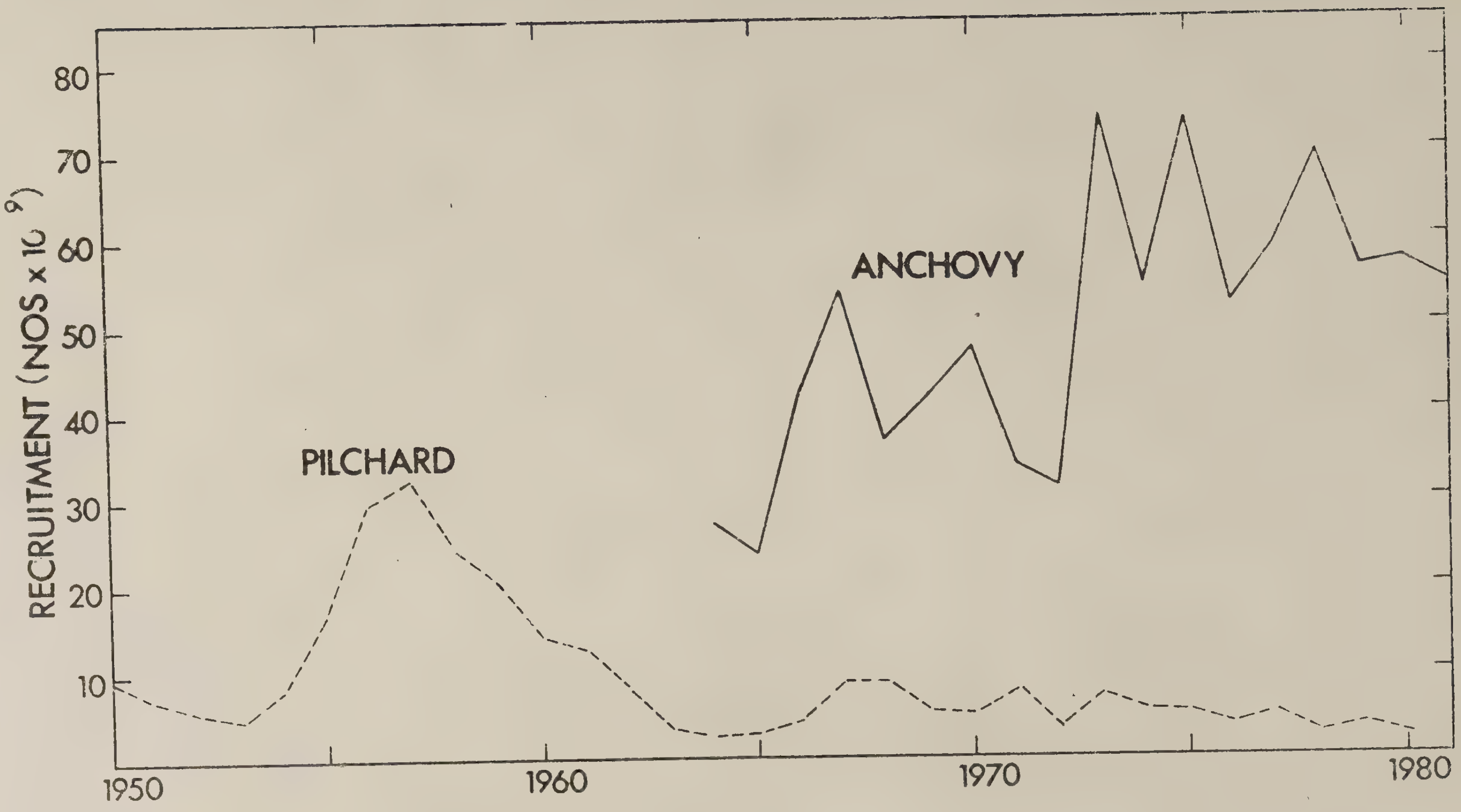


Figure 2. Time series of South African pilchard and anchovy recruitment values from VPA calculation of number of fish alive at 6 months of age.

AGE AT MATURITY

Corresponding to the decline in the pilchard pop lation there has been a substantial change in the length at maturity of fish (Figure 3). During the 1950's and early 1960's 50% maturity occurred at an average caudal length of 18,5 cm, corresponding to an age of four years. After the decline the average length at 50% maturity was reduced to 15,5 cm or two years of age (Crawford, Shelton and Hutchings 1980). There has been an increase in length at 50% maturity in the anchovy (Figure 4) after the increase in biomass that resulted from good recruitment in 1973. Clearly a shorter-lived species like the anchovy has less manoeuvrability in age at maturity than the pilchard.

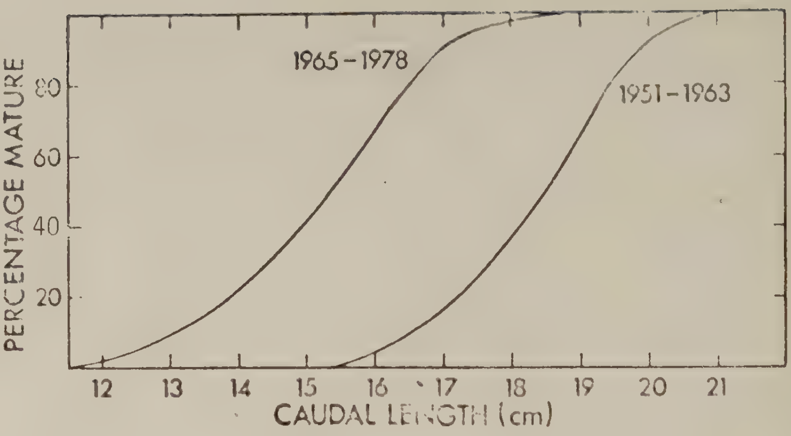


Figure 3. Percentage maturity at length ogives for pilchard sampled during the periods 1951 - 1963 and 1965 - 1978.

GONAD WEIGHT

Bagenal (1973) reported an increase in the mean number of eggs per gram of female body weight with a decrease in the size of pike *Esox lucius* and plaice *Pleuronectes platessa* populations. He considered this to be a compensatory mechanism. Fecundity estimation in clupeoids is complicated by serial spawning and has not been recorded at different population sizes for the South African pilchard. However, gonad weight is easy to measure and monthly mean values are available since sampling commenced in 1950. From the data gonad condition factors (GF) were calculated for four periods during the history of the fishery using the formula:

$$GF = \frac{\text{gonad mass (dg)}}{\text{caudal length (cm)}^3} \times 10\ 000$$

which takes into account increased gonad weight with fish weight. The monthly plots for the four periods (Figures 5 and 6) show a seasonal increase in GF over the summer spawning season, but more particularly, in both females and males there is a clear compensatory increase in GF with the decline in the pilchard population subsequent to 1961.

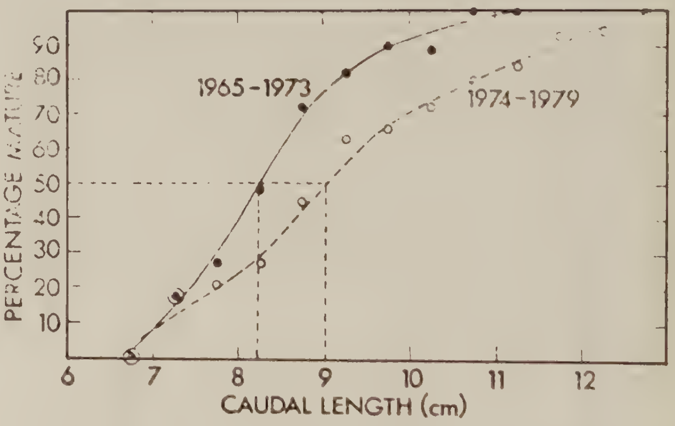


Figure 4. Percentage maturity at length ogives for anchovy sampled during the periods 1965 - 1973 and 1974 - 1979.

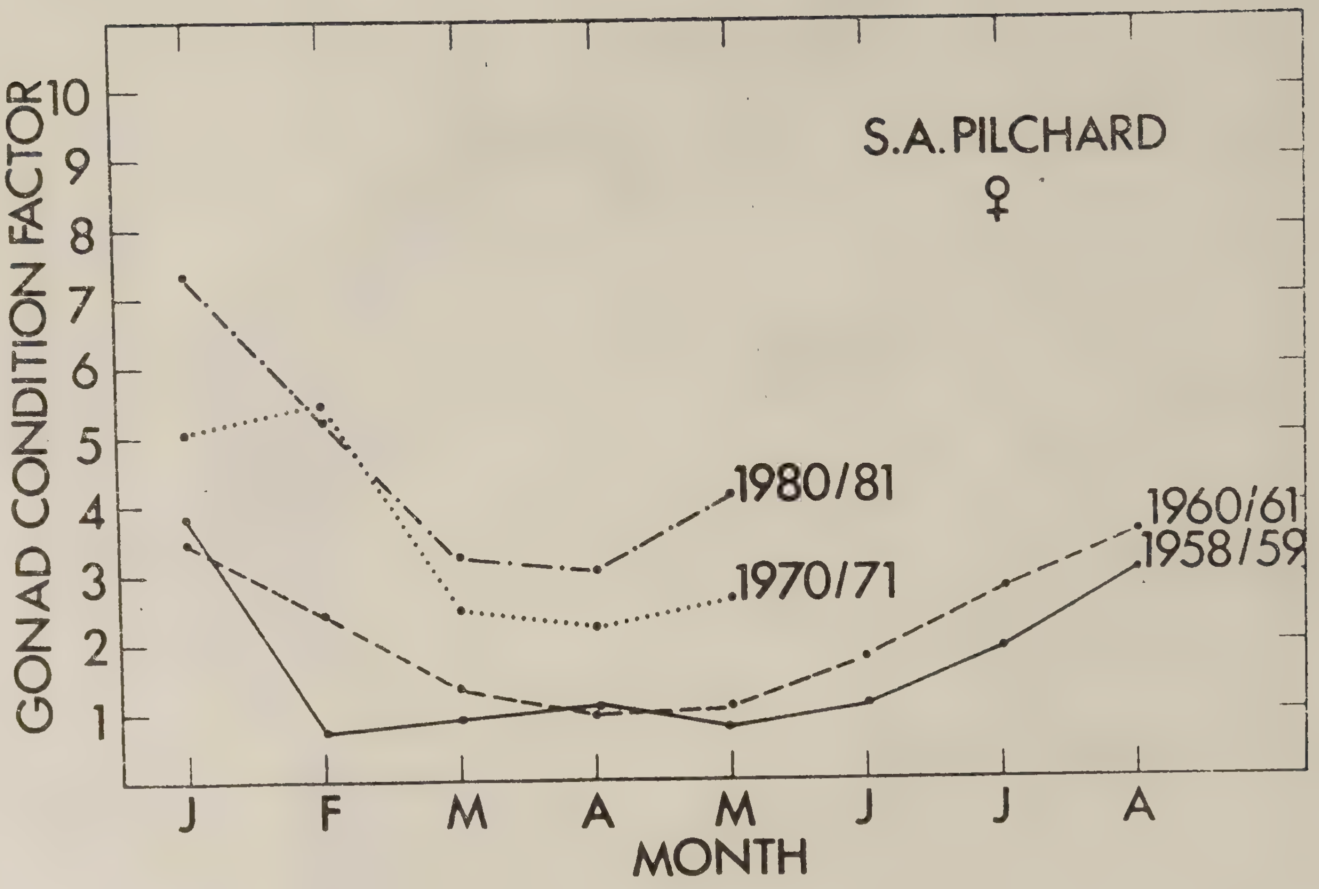


Figure 5. The mean gonad condition factor of mature 15 - 20 cm female pilchard in each month of four different periods during the history of the fishery.

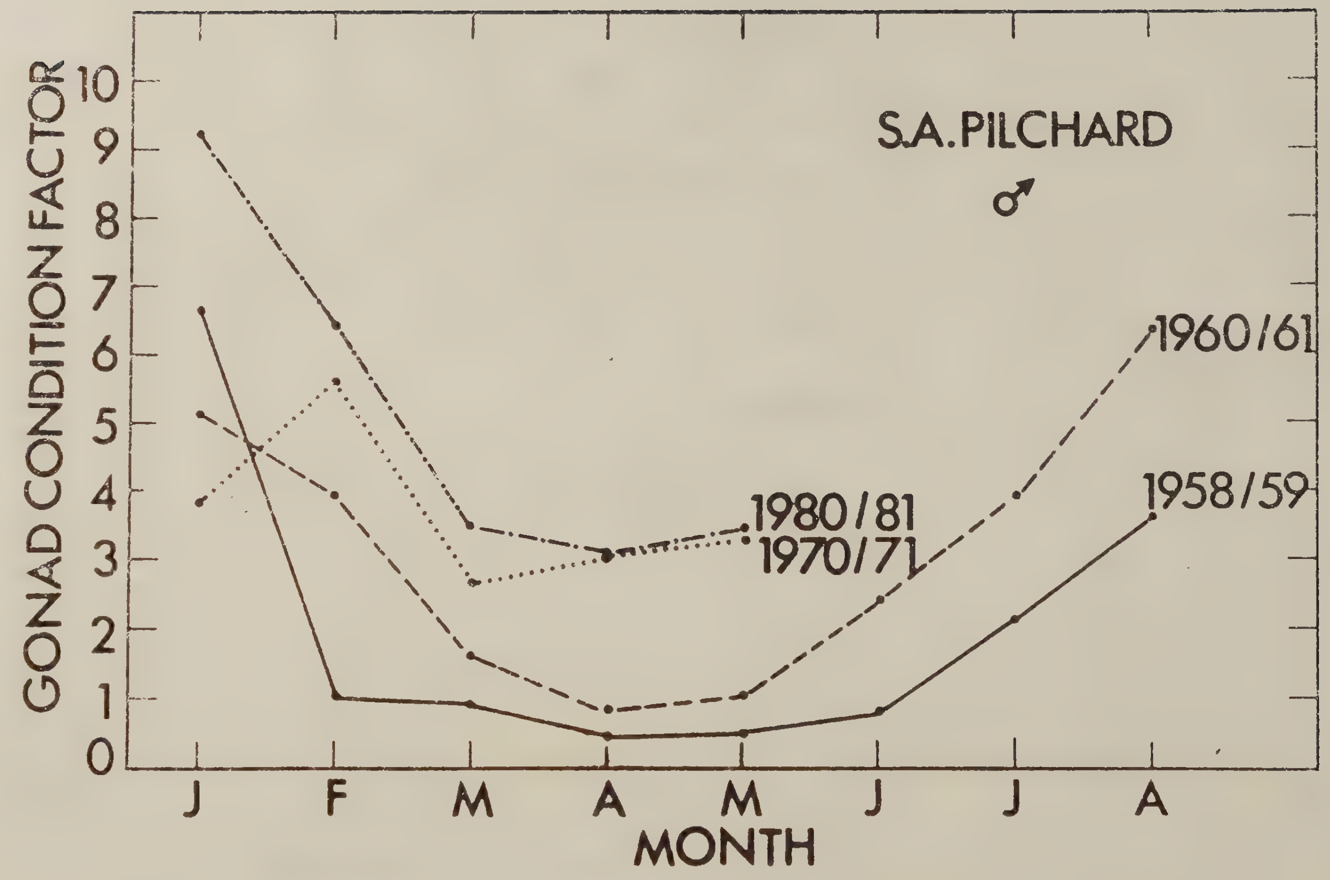


Figure 6. The mean gonad condition factor of mature 15 - 20 cm male pilchard in each month of four different periods during the history of the fishery.

SPAWNING GEOGRAPHY

As a population expands or contracts its range, changes in the spawning locality may occur. In contrast to other eastern boundary current regions, the convexity of the South African coastline splits the southern Benguela system into a warm water southern region and a cold water western region.

In the anchovy, egg production coincides in time with maximum upwelling but is highest in the warm southern region where upwelling is minimal and egg development is rapid (Figure 7). Early stage larvae derive maximum benefit from the equatorward geostrophic flow associated with upwelling (Shelton and Hutchings 1982) to be transported rapidly into the rich plankton region down-stream of the two main upwelling sites. There has been no detectable change in spawning geography after the good recruitment recorded in 1973).

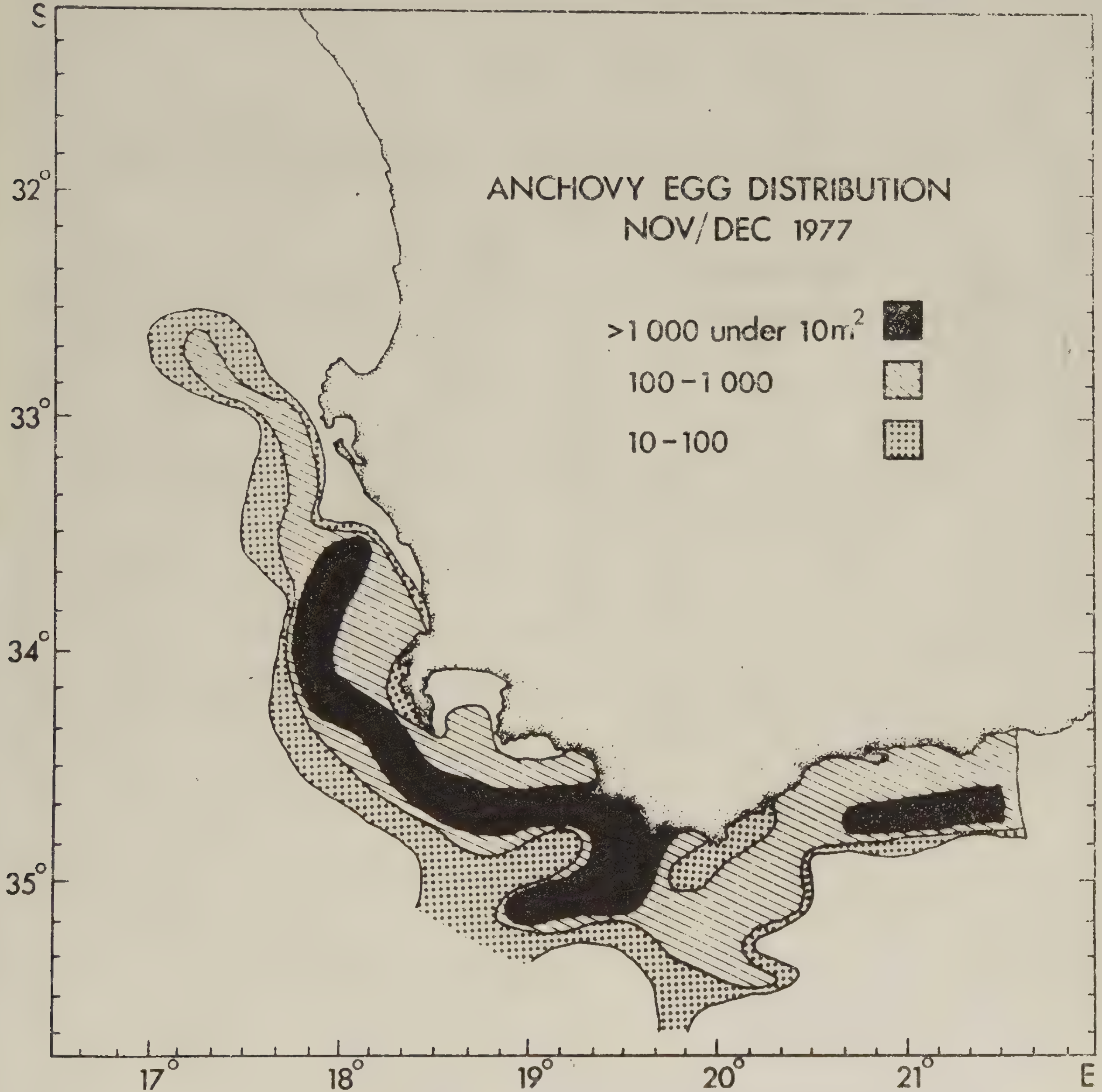


Figure 7. The distribution of anchovy eggs during November and December 1977.

Prior to the pilchard decline, when fish up to nine years old were present in the population, spawning occurred predominantly off the west coast, offshore of the major upwelling region and close to the recruitment ground (Figures 8a). With the decline in population size and the associated reduced age composition and change in the age at maturity, the centre of spawning has shifted to the south (Figure 8b). The change in spawning area may be expected to alter recruitment. The change could only be considered compensatory if survival through to recruitment was favoured. While the more stable structure of the water column in the south may favour spawning and egg development in the depleted population, recruitment still occurs on the west coast and requires favourable larval transport, perhaps more risky than recruitment from west coast offshore spawning at high population size. The reduced pilchard population may derive some benefit from spawning in association with the anchovy since early recruits of anchovy and pilchard frequently shoal together as evidenced by the number of mixed catches (Crawford 1981). A preliminary examination has not revealed an increased incidence of mixed shoaling but comparison is only possible since 1964 when the small-meshed net was introduced, and by this time the pilchard population had already declined.

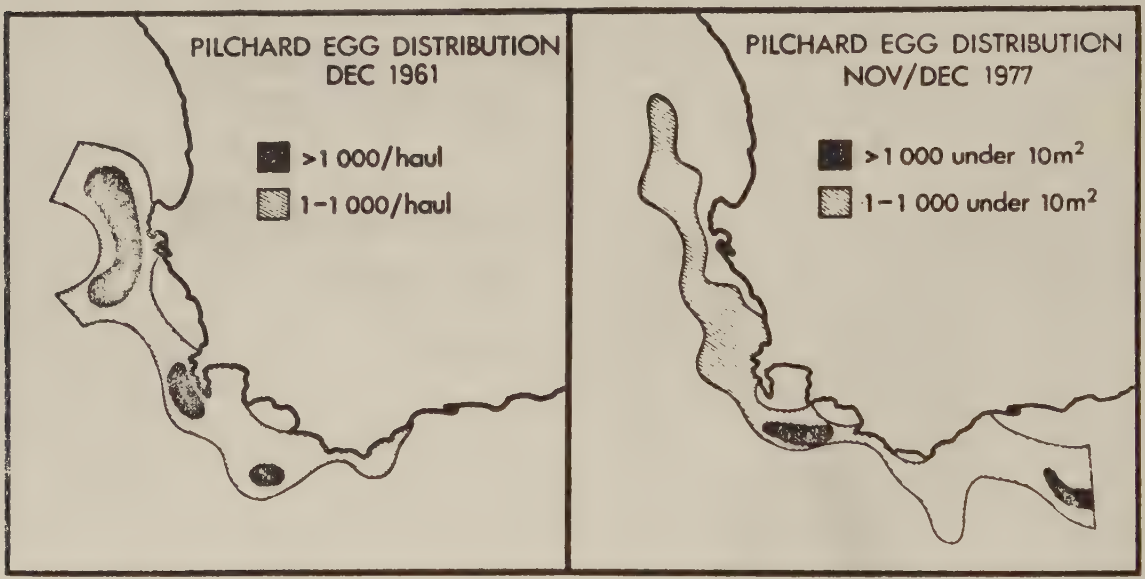


Figure 8. A comparison between pilchard egg distributions during December 1961 and November/December 1977.

CATCHABILITY AND SCHOOLING

The observation by Paloheimo and Dickie (1964) that catch per unit time may depend as much on the size of schools and densities of fish within them as on overall abundance and that there may be an inverse relationship between the catchability coefficient and abundance, has important consequences in density-dependent population regulation. This has been realized by Csirke (1980) who used catch per unit effort as an index (S) of population density in the Ricker equation

$$R = aBe^{-bS} \qquad (2)$$

similarly MacCall (1980) incorporated a coefficient (c) to reduce the effect of the density-dependent term in the Ricker equation

$$R = aNe^{-bN^{c}} \qquad (3)$$

When c = 1 a Ricker curve results, but when c decreases below k the ascending limb of the recruitment curve becomes steeper and more linear, the peak becomes broader and the descending limb becomes progressively shallower. In the South African pilchard and anchovy there is strong evidence of an inverse relationship between catchability and population size (Crawford pers. comm.) (Figures 9 and 10).

Jakobsson (1980) has found that the stock-recruit relationship in Icelandic herring is linear or even depensatory at low population size. Depensatory curves have been considered by Larkin, Raleigh and Wilimovsky (1964), Paulik (1973), Holling (1973), Clark (1974), Gulland (1977), Peterman, Clark and Holling (1979) and Ulltang (1980). Clark (1974) emphasized that when depensation occurs in the recruitment curve a small increase in effort can switch the relationship to an unstable state, leading to extinction. Although the cause may be different, Gulland (1977) regards this effect as similar to that observed when there is an inverse relationship between catchability and collapse. In both instances the equilibrium yield profiles are similar. Ulltang (1980) has observed that the combined effect of the inverse catchability relationship and depensation will rapidly deplete the stock at a catch or effort level above MSY.

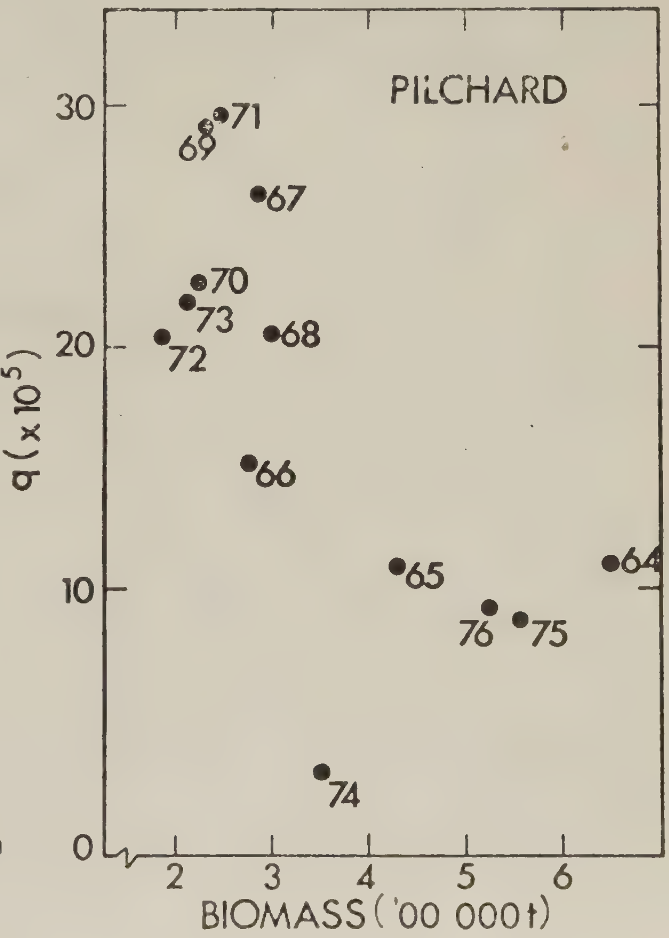


Figure 9. The catchability coefficient of pilchard calculated as weighted F from VPA divided by directed effort and expressed as a function of total pilchard biomass (from Crawford, R.J.M., Sea Fisheries Research Institute).

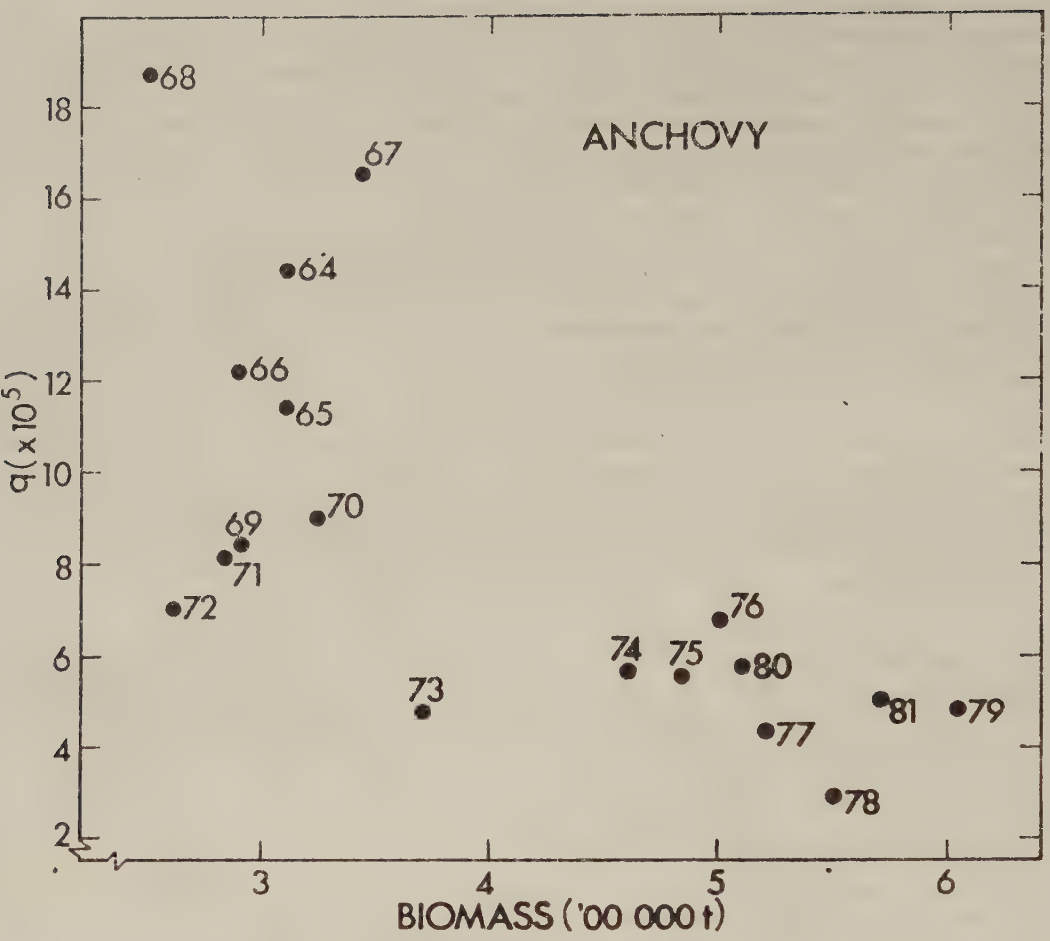


Figure 10. The catchability coefficient of anchovy calculated as weighted F from VPA divided by directed effort and expressed as a function of total anchovy biomass (from Crawford, R.J.M., Sea Fisheries Research Institute).

Increased mortality rates leading to depensation in the recruitment curve at low stock levels may be caused in a number of ways. Those involving the breakdown in schooling, leading to, for example, ineffective egg fertilization or the inability to feed successfully and maintain energy reserves for serial spawning, are attractive. Clark (1974) suggests that since the efficiency of schooling increases with the size of schools, depensation in the recruitment relationship could result from an increase in the rate of juvenile losses to predation at low population levels. If predation on the juveniles is of the Type III form (Holling 1973) then a refuge from predation will occur at low juvenile density, giving rise to a stable equilibrium on the recruitment curve at a low population size (Peterman et al. 1979). Hewitt (1981) has found that in the Californian anchovy, school formation starts at 18 days after hatching. Between this stage and recruitment juveniles could be preyed on by a number of species. In the Benguela system the jackass penguin *Spheniscus demersus* has been recorded eating pre-recruit clupeoids and is capable of switching prey between pilchards and anchovy (Crawford and Shelton 1981) and could thus exert a Type III predatory response on juvenile pilchards. The fact that Smith and Lasker (1978) have not recorded a relationship between large larvae and recruitment in the Californian anchovy supports the idea that recruitment is determined subsequent to the onset of schooling.

THE RECRUITMENT CURVE AND YIELD

The effect of various shapes of the recruitment curve on yield is particularly important at high levels of fishing effort when a further small increase in effort or fishing effort could result in the collapse of the population. In Fig. 11a the solid line is a fairly typical recruitment curve for a clupeoid population which displays an inverse relationship between catchability and population size, as described by equation 3 where c has a value, for examples, of 0.5. This slightly domed recruitment curve corresponds to a symmetrical yield curve. If c takes on a value of 1 the normal Ricker relation results (broken line curve). This has a more domed appearance due to the steeply descending righthand limb resulting from the assumption that the rate of density-dependent mortality (e.g. cannibalism) is directly proportional to spawner biomass rather than density. The maximum yield is greater, but occurs at a lower fishing mortality.

A compensatory decrease in the age at maturity in a depleted population has the effect of decreasing the slope of the replacement line at any F value (Figure 11b, line 1 to line 2). The influence on the yield curve is to displace the righthand limb, allowing a yield to be taken at a higher fishing mortality than would otherwise be possible.

If fecundity varies in a density-dependent compensation manner then the recruitment curve has a more pronounced dome and more steeply sloping limbs (Figure 11c, solid line curve). This means that the maximum yield is larger, is taken at a higher level of fishing mortality and drops off sharply beyond MSY. The incorporation of this effect into the Ricker equation.

$$R = aNe^{-bN^{c}} \tag{4}$$

requires modification of the normally density-independent "a" term, corresponding to environment and fecundity, into a part that is density-independent (a) due to the environment and a part that is density-dependent (g) representing density-dependent changes in fecundity so that

$$g = f(N). \tag{5}$$

The rewritten equation would then take the form

$$R = agNe^{-bN^{c}} \tag{6}$$

Depensation resulting from increased mortality at low population size (Figure 11d, solid line curve) will result in the yield curve suddenly collapsing, and in order to halt this process, fishing mortality must be reduced. This results in an equilibrium yield curve that bends backwards. If the depensation falls below the replacement line at F = 0 then it is termed "critical" (Clark 1974) and the population collapses even in the absence of fishing. Even if the depensation is non-critical, the equilibrium points (e.g. 2) along the backward bending part are not stable and depending which way the population is displaced, it will either collapse or move up to the stable equilibrium (1) on the recruitment curve.

If the recruitment escapes the depensatory trough at some low population size (Figure 11e, solid line curve) then the backward bending of the yield curve will be arrested and a stable equilibrium (3) will be obtained.

In general, the combined effects of an inverse relationship between catchability and population size, a compensatory decrease in the age at maturity and a compensatory increase in fecundity will allow yield to be maintained up to a high level of fishing mortality but will precipitate a rapid collapse at a point only slightly above MSY. When depensation is superimposed on these effects, the collapse is more rapid and recovery will be slower. In some instances a reduced mortality of juveniles at a low population size may arrest collapse and allow a small but stable yield to be harvested.

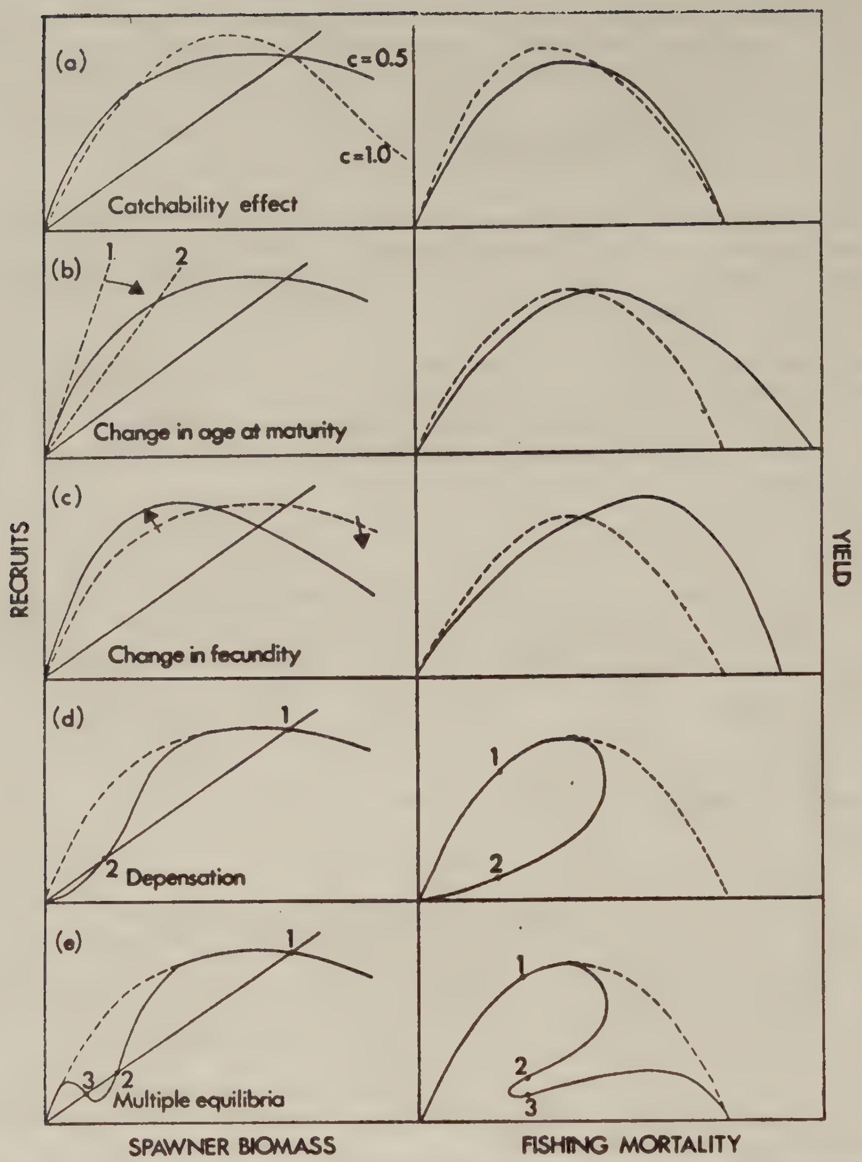


Figure 11. A summary of the effect of density-dependent population responses on the shape of both the stock-recruit and yield curves. Replacement at a relatively low fishing mortality is indicated by the solid diagonal line on the stock-recruit curves.

(a) A comparison between stocks exhibiting the stock-recruit relationship $R = Ne^{-bN}$ where c = 1 (a normal Ricker curve) and c = 0.5 (spawner biomass increasing faster than spawner density).

(b) The effect of reducing age at maturity at low stock sizes. The steeply sloping dashed line (1) represents replacement if no change in maturity has occurred at an equivalent F value.

(c) The effect of a compensatory increase in fecundity as spawner stock is reduced (solid curve).

(d) The effect of depensation in the stock-recruit relationship. A stable equilibrium occurs at 1, but 2 represents an unstable equilibrium.

(e) A stock-recruit curve for a population escaping depensation at a low spawner biomass, for example due to a Type III functional predator response on pre-recruits. Points 1 and 3 are stable equilibria, but point 2 is unstable.

STOCK-RECRUIT PLOTS FOR THE SOUTH AFRICAN ANCHOVY AND PILCHARD

The 18 stock-recruit data points for the South African anchovy fall on the lefthand limb of a shallowly domed recruitment curve with an arbitrary c value of 0.5 (Figure 12). The first two data points, 1964 and 1965, are low and may indicate an underestimate of recruitment since the fishery only partially exploited the stock in the first two years. The points are all well above the replacement line in the absence of fishing (F = 0) but replacement lines in keeping with fishing mortality values before and after the good recruitment of 1973 pass through the respective groups of points. In 1979, 1980 and 1981 recruitment fell below the replacement line and the population appears to be headed back down the lefthand limb of the recruitment curve. Since the topography of the lefthand limb was defined as the population grew and has been shown to be fairly gently sloping, management should be able to prevent collapse provided there is no gross environmental anomaly.

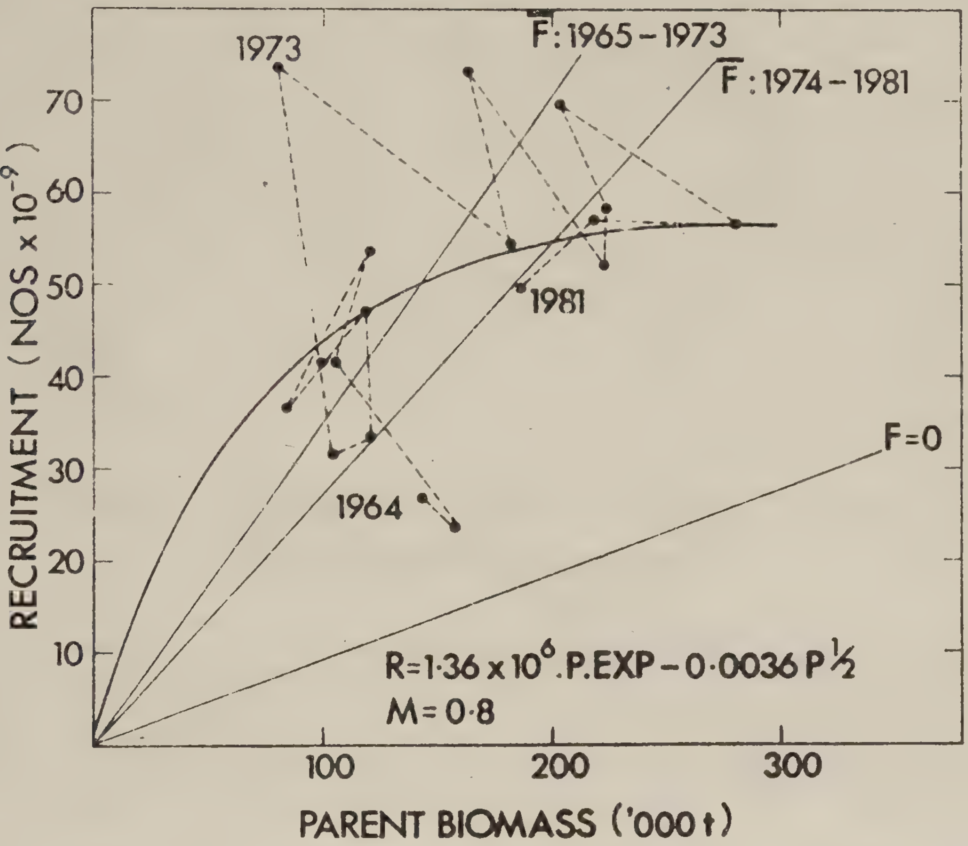


Figure 12. A generalized recruitment curve for anchovy at m = 0,8 where parent biomass is one-year-old fish and older and recruitment is calculated at 6 months of age. Replacement at F = 0 and at average F values during the periods 1965 - 1973 and 1974 - 1981 is shown.

Data points on the pilchard stock-recruit plot (Figure 13) have been differentiated into two groups. The open circles correspond to years before 1965 including the period of high biomass and subsequent decline. The closed circles are for data between 1966 and 1980, a period of relative stability, despite the fact that effort is directed towards this species for canning. The parent biomass axis incorporates the large changes in maturity that have been observed in the population. In the absence of this compensation and at present levels of fishing mortality, the replacement line would have been almost vertical (Figure 13).

The resilience displayed by the pilchard to heavy fishing pressure, having fallen below replacement recruitment on a number of occasions in recent years, cannot easily be explained by a conventional recruitment curve. The resilience may be evidence of a stable equilibrium at a low population size, as described by Peterman et al. (1979) and illustrated in Figure 11e. Even if fishing on the pilchard were to cease entirely, recovery would not be automatic if the lower descending righthand limb were still cut by the F = 0 replacement line. This may explain the lag in the recovery of the Japanese sardine *Sardinops melanostica* and the failure of the Californian sardine *Sardinops caerulea* to recover despite the reduction of fishing pressure.

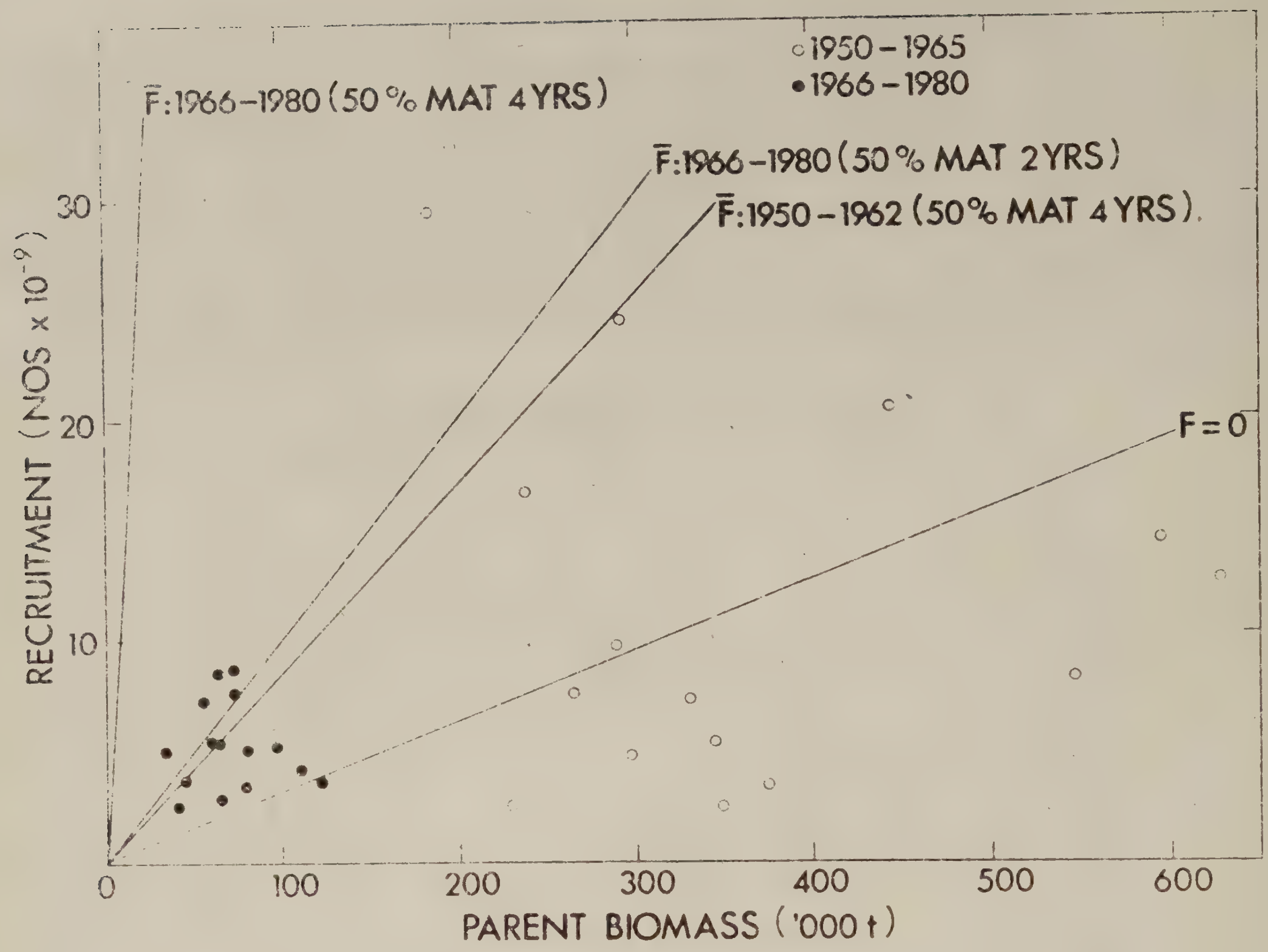


Figure 13. Scatter plot of pilchard recruitment at six months of age against parent biomass (incorporates the density-dependent change in age maturity). Open circles are 1950 - 1965 stock-recruit values and closed circles 1966 - 1980 values. The replacement line at F = 0 applies to the 1950 - 1965 values only; replacementlines at average F for 1950 - 1962 and 1966 - 1980 take into account the change in age at maturity between these periods, but replacement at average F during 1966 - 1980 if age at maturity had not changed is also shown.

STOCK-RECRUIT CURVE AND MANAGEMENT

A curve fitted to a set of stock-recruit points should not be extrapolated beyond those points without caution. Although a Ricker or Beverton and Holt curve can often be fitted to the data, in a stock where fishing mortality is increasing it is the area of extrapolation at lower spawner biomass which could be most significant in determining the pattern of future yields. We maintain that by examining the density-dependent processes that are displayed at intermediate stock sizes a preview of the topography of the recruitment curve at lower stock sizes can be obtained and used in a cautious approach to management. Once a suitably shaped recruitment curve has been decided upon, the incorporation of a stochastic element with a similar variability to that observed in the stock-recruit data points can be useful in determining the potential variability of yields at different levels of fishing mortality.

As an example of this approach Armstrong et al. (1983) used the observed variance in the South African anchovy recruitment as stochastic input into a regenerating yield model. A 100-year run of this model at F = 0,5 is shown in Figure 14. By running the model 50 times over a 20-year time horizon, a long-term mean yield, C.O.V. of the yield and probability of the yield falling below 100 000 tons was determined for a series of F values (Figure 15).

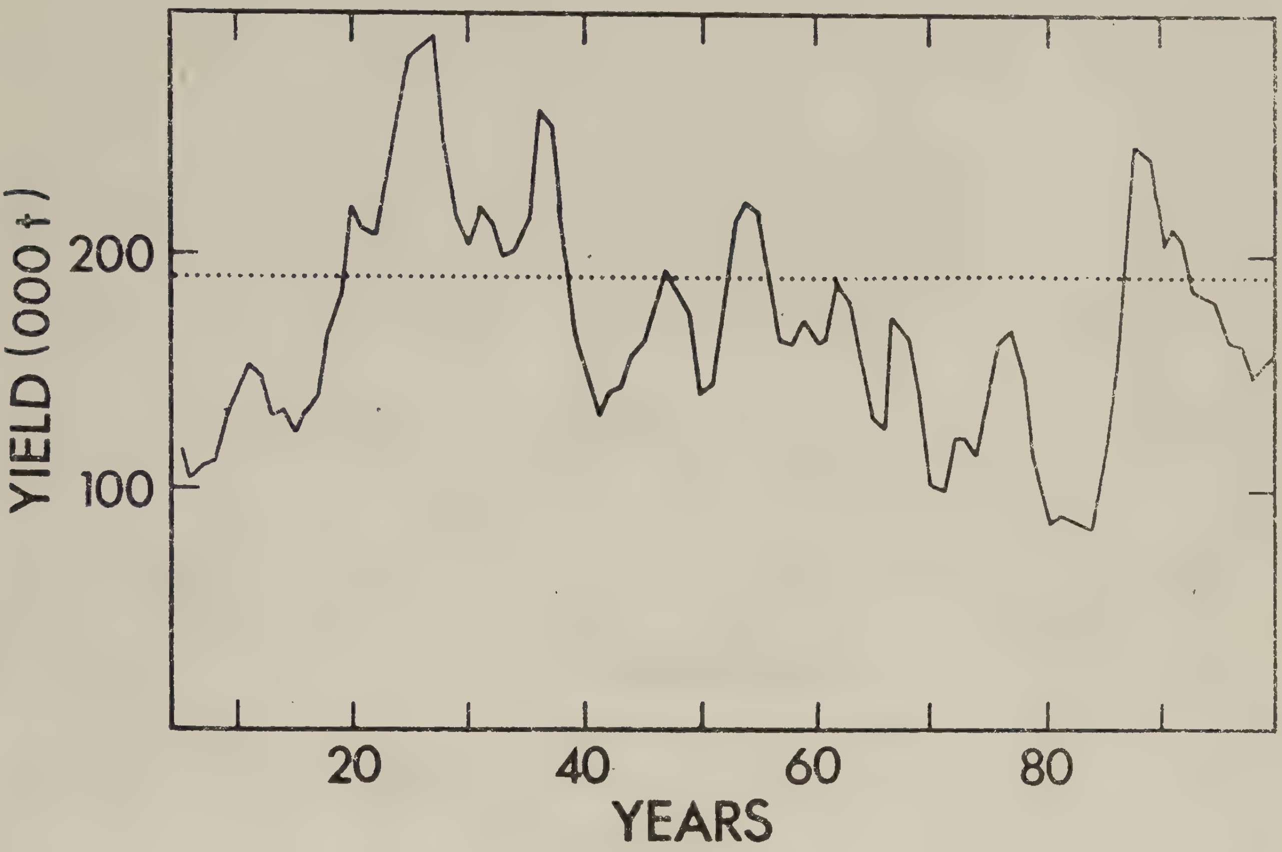


Figure 14. An example 100-year run of a stochastic anchovy yield model at F = 0,5. The stochastic input was derived from the observed deviation of Ln R/N values about a fitted Ln R/N versus $\sqrt{N}$ regression line and hence expresses a normal distribution of Ln a values. The effect of serial correlation in density-independent egg and larval mortality and /or fecundity due to environmental cycles was examined by applying a serial correlation coefficient of 0,5 to the Ln a values (from Armstrong et al., 1983).

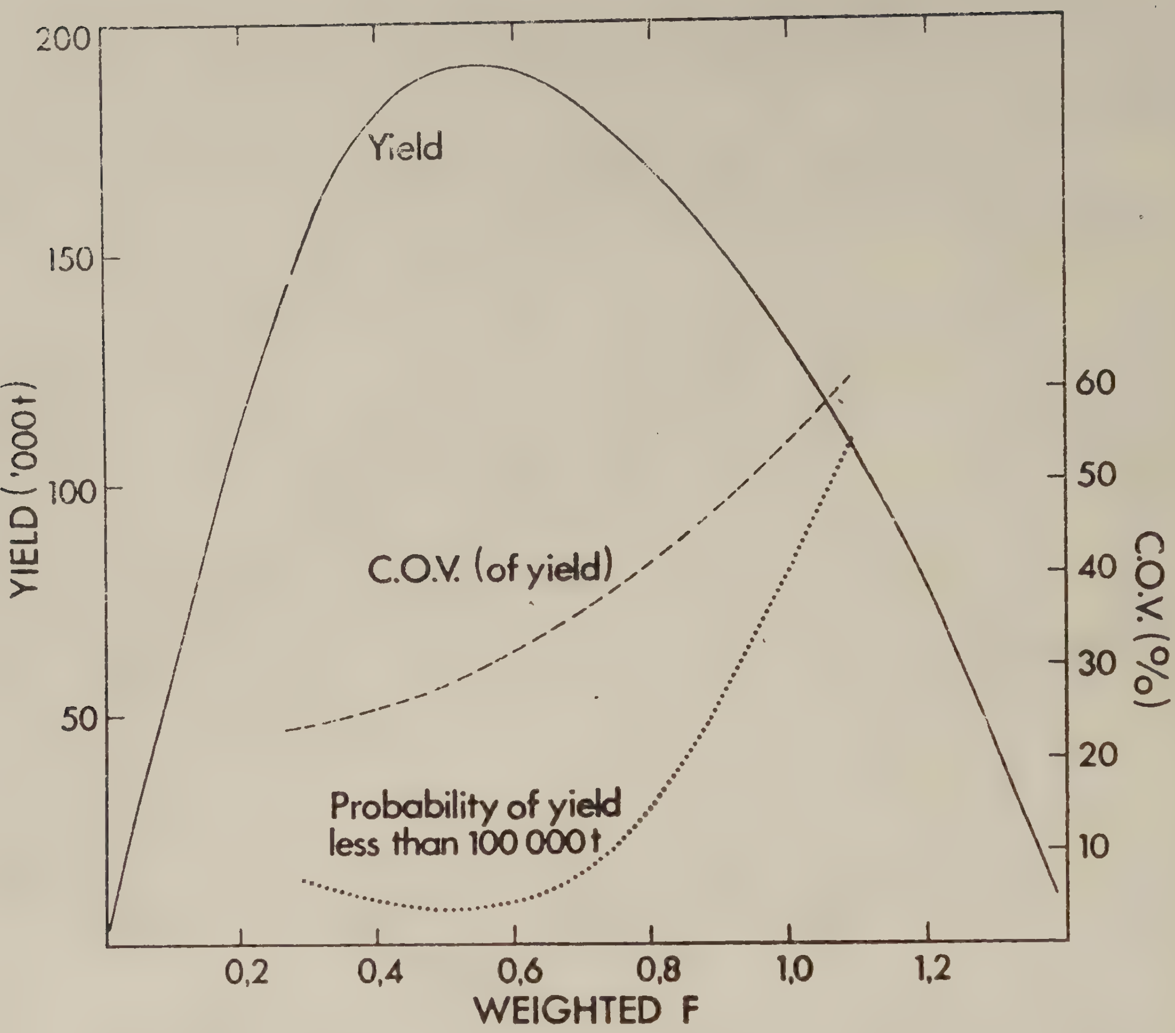


Figure 15. The long-term mean yield curve derived from 50 runs of the stochastic anchovy yield model over a 20-year time horizon. Also shown are the coefficient of variation of the yield and the probability of yield falling below 100 000 tons within 20 years.

CONCLUSIONS

The shape of the recruitment curve has a considerable influence on the average yield that can be taken, particularly at high levels of exploitation.

By examining the density-dependent population responses displayed at intermediate stock sizes, a preview of the shape of the recruitment curve at lower stock sizes can be obtained and used in a cautious approach to management.

In the South African pilchard compensatory changes in age at maturity and in gonad condition factor are important density regulatory responses. In addition, the inverse relationship between catchability and population size may be evidence that spawner density changes at a slower rate than spawner biomass (MacCall, 1980) and hence a conventional Ricker curve of recruits against spawner biomass may overestimate the severity of density-dependent mortality. The influence on the recruitment curve of a contraction in spawning range to the south after the decline of the pilchard is equivocal.

The incorporation of a compensatory change in fecundity into the generalized Ricker equation $R = aNe^{-bN^c}$ requires modification of the "a" term (corresponding to environment and fecundity) into a part (g) that is density-dependent ($g=f(N)$) and a part (a) that is density-independent. The rewritten equation takes the form $R = agNe^{-bN^c}$.

The combined effects of an inverse relationship between catchability and population size, a compensatory decrease in the age at maturity and a compensatory increase in fecundity will allow yield to be maintained up to a high level of fishing mortality but will precipitate a rapid collapse at a point only slightly above MSY. When depensation is superimposed on these effects the collapse is more rapid and recovery will be slower.

Reduced mortality of juveniles at a low population size due to, for example, a Type III predatory response, may give rise to a second stable equilibrium. The relative stability displayed by the South African pilchard population at a low biomass in recent years may be evidence to support the existence of a second equilibrium position.

REFERENCES

Armstrong, M.J., P.A. Shelton, R.M. Prosch and W.S. Grant. 1983. Stock assessment and population dynamics of anchovy and pilchard in ICSEAF Division 1.6 in 1982. Colln.scient.Pap.int.Commn.SE.Atl.Fish. 10:7-25

Bagenal, T.B. 1973. Fish fecundity and its relations with stock and recruitment. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 164:186-198.

Clark, C.W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J.Cons.int.Explor.Mer. 36:7-14.

Crawford, R.J.M. 1981. Distribution availability and movements of anchovy Engraulis capensis off South Africa. 1964-1976. Fish.Bull.S.Afr. 14:51-94.

Crawford R-J-M- and P.A. Shelton. 1981. Population trends for some Southern African seabirds related to food availability. In Proceedings of the symposium on Birds of the Sea and Shore. Cape Town, 1979. (J. Cooper, ed.). Cape Town: Southern African Seabird Group.

Crawford, R.J.M., P-A- Shelton, and D. Hutchings, 1980. Implications of availability, distribution, and movements of pilchard (Sardinops ocellata) and anchovy (Engraulis capensis) for assessment and management of the South African purse-seine fishery. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:355-373.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:307-313.

Gulland, J.A. 1977. The stability of fish stocks. J.Cons.int.Explor.Mer. 37(3):199-204.

Hewitt, R. 1981. The value of pattern in the distribution of young fish. Rapp.P.-v.Réun.Cons.int. Réun.Cons.int.Explor.Mer. 178:229-236.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann.Rev.Ecol.Syst. 4:1-23.

Jakobsson, J. 1980. Exploitation of the Icelandic spring-and summer-spawning herring in relation to fisheries management. 1947-1977. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 1977:23-42.

Larkin, P.A., R.F. Raleigh and N.J. Wilimovsky. 1964. Some alternative premises for constructing theoretical reproduction curves. J.Fish.Res. Bd Canada. 21(3)477-484.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as Engraulis. pp. 201-219. In IOC Workshop Report No. 28 (G.D.Sharp, ed.). IOC/UNESCO, Paris.

Newman, G.G. and R.J.M. Crawford. 1980. Population biology and management of mixed-species pelagic stocks off South Africa. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:279-291.

Paloheimo. J.E. and A.M. Dickie. 1964. Abundance and fishing success. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 155:152-163.

Paulik, G.J. 1973. Studies of the possible form of the stock-recruitment curve. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 164:302-315.

Peterman, R.M., W.C. Clark and C.S. Holling. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems. pp. 321-341. In Population Dynamics (Proceedings of the 20th Symposium of the British Ecological Society London 5-7 April 1978). (R.M. Anderson, B.D. Turner and L.R. Taylor, eds.). Blackwell, Oxford.

Shelton, P.A. and L. Hutchings. 1982. Transport of anchovy, Engraulis capensis Gilchrist, eggs and early larvae by a frontal jet current. J.Cons.int.Explor.Mer. 40:185-198.

Smith, P.E. and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 173:77-84.

Ulltang, O. 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:489-504.

INTERACTIONS OF PELAGIC FISHES AND THE RELATION BETWEEN ENVIRONMENTAL FACTORS AND ABUNDANCE

by

Bernard Einar Skud

U.S. National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Center
Narragansett Laboratory
South Ferry Road
Narragansett, Rhode Island 02882
USA

Resumen

Los biólogos pesqueros han notado que las correlaciones entre factores físicos del ambiente y la abundancia de peces fallan con frecuencia. Las explicaciones para estas fallas han generalmente asumido que los datos para la comparación fueron inadecuados o que las relaciones fueron fortuitas o engañosas. El examen de las medidas de la abundancia y los factores ambientales de la caballa del Atlántico (*Scomber scombrus*) y la sardina de California (*Sardinops sagax caerulea*) indican que la falla de estas correlaciones ocurren cuando las especies cambian del componente dominante al componente subordinado de la biomasa total de pelágicos. Cuando especies que compiten, tales como el arenque del Atlántico (*Clupea harengus*) y la anchoveta de California (*Engraulis mordax*), tomaron la dominancia, su abundancia fue correlacionada positivamente con los mismos factores ambientales. La relación para especies subordinadas fue negativa. Un cambio similar en la dominancia y una relación inversa con los factores ambientales fue reportada para guppy (*Poecilia reticulata*) y para el *Xiphoronorus maculatus* en estudios experimentales. Aun cuando los cambios en dominancia no podrían explicar todas las fallas de las correlaciones, los estudios de la relación entre el ambiente y la abundancia deben considerar la densidad de las especies que compiten entre ellas y en particular la posición de las especies en la jerarquía de la dominancia.

INTRODUCTION

"All correlations fail eventually." This facetious adage has been credited to Lionel A. Walford, but has been echoed by others who have examined the durability of correlations between physical factors of the environment and the abundance of fishes. Gulland (1978) remarked how few of these correlations had stood the test of time. Ware and Henriksen (1978) commented that" . . . Every scientist knows that the path of fisheries research is littered with the bones of similar correlations that have been eventually proven spurious. . . ." Akenhead (1981) said that, without a mechanistic model, such correlations can be expected to fail as conditions extended to the correlation change. Cushing (1978) summarized the situation as follows: "Although it is clear that climate, in a general sense, affects fish stocks, the nature and mechanisms of the relation are not well understood. Attempts at direct empirical correlations between environmental factors and year-class strength have seldom been successful because of the wide choice of factors and the limited number of observations . . . It seems that we need a deeper understanding of the various biological and physical events in the ocean and their links to the factors directly controlling year-class strength."

I will discuss examples of these correlations that have failed. My intent is to show that these "failures" should not be summarily dismissed on the assumption that the data were faulty, that the criteria for comparison were ill-founded, or the relation spurious, rather that, with the usual contraints of accepting or rejecting an hypothesis, the results should stimulate the questions: How? and Why?

ATLANTIC MACKEREL AND TEMPERATURE

Taylor et al. (1957) correlated mackerel, *Scomber scombrus*, landings with air temperature data and reported a positive and highly significant relation from 1820 to 1890, but thereafter the relation was not significant. McHugh (1976) considered this 70-year correlation of particular note, because annual mean temperatures showed no particular trend prior to 1900, but did show a marked increase thereafter. Taylor et al. (1957) concluded that there was nothing in the temperature record to account for the precipitous decline of mackerel in the 1880's and the continued low abundance in the 1900's.

Bell and Pruter (1958) reexamined the mackerel data and compared temperature records from the open ocean (Riehl, 1956) with fluctuations in the landings from 1880 to 1930. Their results (r=-0.15) confirmed the insignificant relation for this period, but the authors questioned the methodology used by Taylor et al. (1957). Bell and Pruter stated:

> ". . .The authoritative study of Sette and Needler (1934) /Sic/ judiciously leaves the question of specific cause or causes of catch fluctuations in Atlantic mackerel unanswered. If a relationship between temperature and mackerel is to be demonstrated, it seems that it should have been more noticeable during the recent period when temperatures rose to a new higher level than during the earlier years (1820-1890) when, although fluctuating, the long-term trend of temperature was relatively level."

Following the lead of Lett and Kohler (1976), Winters (1976) and Ware and Henriksen (1978), who reported a competitive interaction between mackerel and herring, *Clupea harengus*, in the Gulf of St. Lawrence during the 1960's, Skud (1982) examined the relation of the two species prior to 1960 in the Gulf of Maine and in the Canadian maritime provinces. His results supported the findings of a competitive interaction in the Gulf of St. Lawrence. He found that landings of the two species were negatively correlated and observed that the decline of mackerel in the 1880's was coincident with an increase in the landings of herring. Based on the conclusion that the species were competitive, Skud (1982) reexamined the relations of landings with temperature. He confirmed the positive relation before 1900 (Taylor et al., 1957) and found a significant, negative correlation for mackerel from 1906 to 1960. During the same period, the relation between herring landings and temperature showed a significant and positive correlation. After 1960, when the abundance of herring declined and the abundance of mackerel increased to its highest level since the decline of the 1830's, the relation between abundance and temperature was negative for herring and positive for mackerel, however, the periods of dominance for each species was too short to test the significance of the correlations.

From this analysis and the study of other species, Skud (1982) concluded that in competing species, the dominant responded positively to changes in the environment that improved survival, and that the subordinate species responded negatively to the same factors. If dominance changed, the response of the two species also changed. He concluded that the dominant species control the abundance of the subordinate and therefore negated or masked the "normal" response of the subordinate to environmental change. He explained the failure of the mackerel-temperature relation reported by Taylor et al. (1957) as a change from the dominant to a subordinate pelagic species.

PACIFIC SARDINE AND SALINITY

A change comparable to that of the herring-mackerel complex also occurred with the California sardine, *Sardinops sagax caerulea,* and anchovy, *Engraulis mordax.* As the abundance of larvae and stock size of sardines declined after 1940, the abundance of anchovy larvae and adults increased (Smith 1972). The deposition of fish scales in marine sediments showed similar fluctuations since 1940 and provided estimates of abundance for both species since 1810 (Soutar and Isaacs 1969). "Most if not all investigators have found the hypothesis that the Pacific sardine and northern anchovy are direct competitors unavoidable. This hypothesis is not supported by the less-than-significant positive correlation between the scale deposition of the two species in the Santa Barbara sediment. . ." (Soutar and Isaacs 1974).

Radovich and MacCall (1979) summarized the status of the research on the sardine-anchovy complex as follows:

> "The hypothesis of interspecific competition from the Pacific sardine . . . has been evoked (Murphy 1966), seemingly verified (Silliman 1969), and set back (Soutar and Isaacs 1974). Smith (1972) showed the anchovy population to have been relatively large (between 2 and 3 million tons) in 1940 and 1941. Such a population size at a time when sardines were also abundant is utterly inconsistent with the competition hypothesis."

Soutar and Isaacs' (1974) data showed that a third species, Pacific hake (*Merluccius productus*), dominated the pelagic biomass during most of the period of record, but its fluctuations in abundance were not considered in the interpretation of the correlation between sardine and anchovy. For example, the abundance of these two species increased from 1905 to 1925 (a strong positive correlation), when the abundance of hake declined 80%. This change suggests that the two species interact with hake and the long-term, positive correlation between sardine and anchovy may have occurred because of the decline in the pelagic biomass. That is, total biomass may have a greater effect on the abundance of sardines and anchovy than the competition between them.

The size of the anchovy population in 1940 and 1941 was large relative to the years after 1925, but Soutar and Isaacs' (1974) data show that it was small relative to the period from 1810 to 1925. The sardine population in 1940 and 1941 also was small relative to earlier years. Comparable levels of abundance, when both populations and the total pelagic biomass were low, is not inconsistent with the hypothesis of competition as claimed by Radovich and MacCall (1979). Levels of abundance of two competing species will be comparable, at some intermediate level, whenever there is a change in dominance. The period most inconsistent with the hypothesis occurred at the turn of the century when the combined abundance of anchovy and hake was approximately half of its maximum, and the high abundance of anchovy in the 1880's occurred when both sardine and hake populations were low. For these reasons, and because all three species apparently interact, I do not agree that the hypothesis of competition can be dismissed.

Bogdanov (1968) also reviewed the sardine-anchovy complex. He made particular reference to the positive correlation (+0.845) between salinity and the recruitment of sardines from 1934 to 1941 (Walford 1946), and the negative correlation (-0.639) for the same factors from 1942 to 1955 (Marr 1960). The change was assumed to be evidence of a fortuitous relation except by Bogdanov (1968), who considered this change to be of paramount importance and extensively reviewed the relations of salinity, upwelling and temperature. Although he did not resolve the question, his astuteness merits recognition, because the change in the correlation was associated with the change in dominance. Recruitment of sardines declined steadily after 1940 and anchovies attained dominance of the pelagic biomass during the latter period.

The change in the relation of the abundance of sardines to salinity was also apparent in the relation to temperature. In the earlier papers that discussed the cause for fluctuations in the abundance of sardines, I was unable to locate any specific reference to a correlation with temperature. As this is the environmental factor that is most frequently used in such studies, I assume that attempts were made, but that results showed a negative relation and, therefore were not reported. Using data from Radovich (1961), Ahlstrom (1965) and Murphy (1977), I compared the catch and catch-per-unit effort (CPUE) with sea-surface temperatures (Table 1). The responses of both species to temperature were inverse to that of salinity. These two factors are associated with upwelling and are themselves inversely related (Bogdanov, 1968). Bakun (1973) computed annual upwelling indices for the California coast (36°N, 122°W). The correlations of these indices with the abundance of sardine and anchovy larvae from 1951 to 1959 were -0.630 and +0.592, respectively. The inverse relation of the two species to these environmental factors and the change in response with the change in dominance support the thesis formulated from the herring and mackerel data (Skud 1982).

Table 1. Correlations of temperature and indices of abundance of sardines and anchovies. (Catch and catch per unit effort for adults and numbers per unit of water strained for larvae.).

		Dominant Species	Sardine		Anchovy	
			CPUE	Catch	CPUE	Catch
Adults:						
1932-1939	(8)	S	-.421	-.410	----	+.353
1940-1947	(8)	A	+.649	+.520	----	-.655
1941-1959	(19)	A	----	+.863**	----	-.560*
Larvae:						
1951-1959	(9)	A	-.710*	----	+.801**	----

I also examined Silliman's (1975) experimental studies on guppy (*Poecilia reticulata*) and swordtail (*Xiphorphorus maculatus*) in which he recorded the actual numbers and biomass of each species. The relation of the two species to temperature was inverse and changed when dominance changed.

DISCUSSION

I concluded that a change in dominance explained the failure of the mackerel-temperature and sardine-salinity correlations (Skud 1982) and I think dominance is one of the unknown mechanisms which Cushing (1978) said was needed to understand the factors controlling year-class strength. As a corollary to the statement by Backiel and LeCren (1967)" . . . that studies of environmental influences on fish growth are of little relevance without data on population density . . . .", I conclude that studies of the relation of environmental factors to abundance for a given species should always consider the density of the competing species, i.e., the social hierarchy.

Not only may a change in dominance explain a change in the correlation with an environmental factor, it may also explain why the indices of abundance of the same or similar species are positively correlated in one area and not another, for example herring and mackerel in the Gulf of Maine and in the Gulf of St. Lawrence after 1960; and for cod and haddock across the North Atlantic (Carrod and Colebrook, 1978). Dominance may also explain certain observations concerning exploited stocks and the effects of fishing. Austin and Ingham (1978) echoed the conclusions of other scientists stating that"

. . . A heavily fished or overfished stock is more susceptible to environmental fluctuations than is a more stable or underutilized stock. . . ." I suggest that a heavily fished stock is likely to be the dominant species and is more responsive to environmental change because it is below its equilibrium density, whereas the underutilized stock is subordinate and its fluctuations in abundance are controlled by the dominant species rather than environmental factors.

I assume that multispecies interactions, rather than two-species complexes, are the norm and that the other species, including predators, also can influence the apparent relation of environmental factors to abundance. Thus in modelling a multispecies complex, it would be necessary to incorporate the effects of a change in dominance from one species to another, along with interactions such as predation and an array of environmental factors.

Just as comparisons between species abundance and environmental factors should be made in concert with other species, so should comparisons of species abundance. Correlation matrices such as presented by Dow (1977), Sutcliffe et al. (1977), Garrod and Colebrook (1978) and Sissenwine et al. (1979) fulfill this basic need, but it is necessary to determine the position of dominance within each trophic level to interpret the meaning of each correlation and of correlations with like and different signs. Without the determination of dominance, correlations of different signs cannot be assumed to represent different responses to an environmental factor or an indication of competition, nor can correlations of a similar sign be assumed to imply similar responses. For example, differences in dominance may explain, as Garrod and Colebrook (1978) showed, why the recruitment of a species is positively correlated with the environment in one geographic area and negatively in another, or why recruitment of species with totally different early life histories had a strong affinity to a given environmental variable.

This varying response of a species probably has contributed to the polarization of the scientific community into two camps as described by Dickie (1973); one crediting major changes in yield to exploitation, the other, relating these changes to the environment. Part of the problem, as Daan (1980) pointed out is that well-documented cases of species replacement refer to heavily exploited populations, so that the effects of fishing are superimposed upon and can never be well-separated from environmental effects. Determination of dominance should help to separate these effects and properly identify species interactions and perhaps, to define the operative mechanisms that have been so elusive.

The effects of interactions discussed in this paper reinforce Burkenroad's (1951), McHugh's (1959), and others' suggestions for an ecosystems approach. And my message is simply that if a long-term significant correlation fails, it is not necessarily because the measure of abundance was inadequate or the hypothetical relation was not biologically justified, etc. The change should be a signal to reexamine the data and to examine factors that could have influenced the relation. Correlation analysis can be a useful tool, it should not be abandoned or condemned, if the results do not support the original hypothesis. The cautions that Bell and Pruter (1958), Austin and Ingham (1978), Akenhead (1981), and others have expressed concerning correlation analyses and their interpretations still pertain. However, the effects of dominance show that the loss of significance or a change in the response is not acceptable evidence that an environmental factor did not affect abundance or that the observed relation was spurious. Nor is it valid, before considering the social hierarchy, to dismiss a correlation for one species when another, in the same trophic level, has not shown a similar response or if the same species when another, in the same trophic level, has not shown a similar response or if the same species did not respond in the same way in a different area. These conclusions do not imply that all correlations that fail are the result of a change in dominance, rather, they support Bogdanov's (1968) approach. He considered the change in the relation between salinity and the abundance of the California sardine to be one of particular significance and although he did not resolve the change, he attempted to explain the phenomenon, rather than assuming that there was a problem with the data or that the relation was fortuitous.

REFERENCES

Ahlstrom, E.H. 1965. A review of the effects of the environment of the Pacific sardine. Int.Comm.Northw.Atl.Fish.Spec.Publ. 6:53-74.

Akenhead, S.A. 1981. Fisheries Oceanography and the nature of carrying capacity for larval marine fishes. Northw.Atl.Fish.Org. SCR Doc. 81/IX/142, 27 p.

Austin, H.M. and M.C. Ingham. 1978. Use of environmental data in the prediction of marine fisheries abundance. pp. 93-89. In Climate and Fisheries. Univ. R.I., Center for Ocean Management Studies.

Backiel, T. and E.D. LeCren. 1967. Some density relationships for fish population parameters. pp. 261-293. In The Biological Basis of Freshwater Fish Production (S.D. Gerking, ed.). John Wiley and Sons.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S.Nat.Mar. Fish.Serv. Tech.Rep.SSRF-671:103 p.

Bell, F.H. and A.T. Pruter. 1958. Climatic temperature changes and commercial yields of some marine fisheries. J.Fish.Res.Bd.Canada. 15(4):625-683.

Bogdanov, G.A. 1968. Factors governing the reproduction of certain sardines. Prob.Ichthy.(USSR). 8(5):695-704.

Burkenroad, M.D. 1951. Some principles of marine fishery biology- Publ.Tex.Inst.Mar.Sci. 2(1):177-212.

Cushing, D.H. 1978. Climatic variation and fisheries. In Problems and Progress in Oceanography Relevant to Fisheries (J.A. Gulland, ed.) FAO Fish.Rep. (206)(Supplement 1) Appendix 2:18-19.

Daan, N. 1978. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. J.Cons.int.Explor.Mer. Symposium on the biological basis of pelagic fish management, No. 24. Rapp.P-v.Réun.Cons.int.Explor.Mer. 177:405-423.

Dickie, L.M. 1973. Interaction between fishery management and environmental protection. J.Fish.Res.Bd.Canada. 30(12):2496-2506.

Dow, R.L. 1977. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. J.Cons.int.Explor.Mer. 37(3):274-280.

Garrod, D.J. and J.M. Colebrook. 1978. Biological effects of variability in the North Atlantic Ocean. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 173:128-144.

Gulland, J.A. 1978. Problems and progress in oceanography relevant to fisheries. FAO Fish.Rep. (206)(Supplement 1):9-21.

Lett, P.F. and A.C. Kohler. 1976. Recruitment: A problem of multispecies interaction and environmental perturbations with special reference to Gulf of St. Lawrence Atlantic herring (Clupea harengus harengus). J.Fish.Res.Bd.Canada. 33(6):1353-1371.

Marr. J. 1960. The causes of major variations in the catch of the Pacific Sardine Proc.World Sci. Meeting. Biol.Sardines. FAO III:667-791.

McHugh, J.L. 1959. Can we manage our Atlantic coastal fishery resources? Trans.Am.Fish.Soc. 88(2):105-110.

____________. 1976. Effects of climatic change on fisheries. Sea Grant Reprint Series. Mar.Sci.Res.Con., St. Univ. N.Y. at Stony Brook Contrib. No. 177:8 p.

Murphy, G.I. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc.Calif.Acad. Sci., Ser. 4. 34(1):84 p.

____________. 1977. Clupeoids. pp. 283-308. In Fish Population Dynamics (J.A. Gulland, ed.) J.Wiley, N.Y.

Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperature. Cal.Fish Game, Fish.Bull. 112, 62 p.

Radovich, J. and A.D. MacCall. 1979. A management model for the central stock of the northern anchovy, Engraulis mordax. Calif.Coop.Oceanic Fish.Invest.Rep. XX:83-88.

Riehl, H. 1956. Sea surface temperatures of the North Atlantic, 1887-1936. Proj. NR 082-120, Office of Naval Research. Univ. of Chicago, Dept. of Meterology. 129 p.

Sette, O.E. and A.W.H. Needler. 1934. Statistics of the mackerel fishery off the east coast of North America, 1804-1930. U.S.Bur.Fish., Investig.Rep.No.19. 48 p.

Silliman, R.P. 1969. Population models and test populations as research tools. Bio.Science. 19:524-528.

____________. 1975. Experimental exploitation of competing fish populations. Fish.Bull.U.S. 73(4):872-888.

Sissenwine, M.P., B.E. Brown, J-E- Palmer and R.J. Essig. 1979. An empirical examination on population interactions for the fishery resources off the Northeastern USA. Workshop on "Multi-species fisheries management advice." St. John's, Newfoundland. 27 pp. (Mimeo).

Skud, B.E. 1982. Dominance in Fishes. The relation between environment and abundance. Science. 216:144-149.

Smith, P.E. 1972. The increase in spawning biomass of northern anchovy, Engraulis mordax. Fish.Bull.U.S. 70:849-874.

Soutar, A. and J.D. Isaacs. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. Calif.Coop.Oceanic Fish.Invest. Rep. 13:63-70.

____________. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish.Bull.U.S. 72(2):257-273.

Sutcliffe, W.H., Jr., K. Drinkwater and B.S. Muir. 1977. Correlations of fish catch and environmental factors in the Gulf of Maine. J.Fish.Res.Bd.Canada. 34(1):19-30.

Taylor, C.C., H.B. Bigelow and H.W. Graham. 1957. Climatic trends and the distribution of marine animals in New England. U.S.Fish.Wildl.Serv.Fish.Bull. 57(115):289-345.

Walford, L. 1946. Correlation between fluctuations in abundance of the Pacific sardine and salinity of sea water. J.Mar.Res. VI(1):48-53.

Ware, D.M. and B.L. Henriksen. 1978. On the dynamics and structure of the Southern Gulf of St. Lawrence herring stocks. Can.Fish.and Mar.Ser. Tech.Rep.No. 800:83 p.

MANAGING VARIABLE FISHERY STOCKS IN AN UNCERTAIN ENVIRONMENT

THE DESIGN OF FISHERY MANAGEMENT SYSTEMS

by

B.J. Rothschild

and

D. G. Heimbuch

University of Maryland
Chesapeake Biological Laboratory
Box 38, Solomons
Maryland 20688
USA

Resumen

La extensión de la jurisdicción de los países costeros ha hecho que se ponga un mayor énfasis en la ordenación de pesquerías. A pesar de este énfasis todavía se han explorado muy poco los modelos que toman en consideración todo el proceso de ordenación en términos de la incertidumbre de la relación stock-reclutamiento, la información requerida para la ordenación, y la estrecha interrelación entre la información para la ordenación y el funcionamiento de la ordenación misma. En este trabajo se desarrolla un modelo basado en estos elementos.

El trabajo describe los elementos fundamentales en la toma de decisiones (un evento casual, una acción de manejo, el saldo de una cuenta, etc) y muestra cómo estos pueden ser conectados para constituir una estrategia de manejo. El trabajo muestra como la estrategia de manejo y el desempeño del manejo pueden ser afectados a través de la obtención de información adicioanl; se proporciona un esquema para evaluar los beneficios de información adicional (por ejemplo, proveniente de reconocimientos de campo y el uso de correlaciones ambientales) relacionadas a los costos de la información adicional.

Se pueden seleccionar estrategias de manejo alternativas por medio de varios criterios. Aquéllos considerados en este trabajo son el máximo y mínimo, valor monetario esperado y utilidad.

El trabajo muestra la construcción y evaluación de diez diferentes estregias; estas se diferencian en si son normativas o adaptables, en si toman o no en cuenta colapsos catastróficos de los stocks, y si toman en cuenta muestreos intensivos o limitados o programas de investigación. De momento, el principal valor práctico del modelo es en (1) demuestra la interrelación íntima de la performance de la ordenación y la información·(2) proporciona las bases para el diseño de un sistema de manejo e información de la pesquería sobre una base cuantitativa y (3) proporciona los medios por los cuales la adquisición de información y toma de decisiones de la ordenación de pesquerías pueden ser armonizadas.

INTRODUCTION

The advent of extended jurisdiction has generated considerable concern for the management of fisheries and considerable rhetoric on the nature of fisheries management and its objectives. Most of the concern, however, has not focused on management *per se* (see, FAO 1980). Rather, it has focused on various important, but relatively *specialized* topics such as optimum yield versus maximum sustained yield, data requirements for management, multiple-species management, preventing stock collapses, satisfying economic and social development requirements of small-scale fisheries, and development of various economic approaches to management, such as fishing-effort limitation. Unfortunately, the studies and activities relating to these topics have not been undertaken in concert; rather each has been emphasized at various times and this has detracted from developing an approach which considers management as an entity in its own right.

Because of this, the important technical topics enumerated above have tended to become side issues and management remains a political process that operates with only a very limited knowledge base. As a result, the long chain of management decisions tends to be disjointed, oriented toward no particular purpose, and inefficient with respect to yielding benefits to society.

Obviously, recovery from this state of affairs will require conceptual foundations for linking together all management decisions. The greatest utility of this conceptual foundation will be to provide a basis for interrelating information needs, the multiple decisions that need to be made in an uncertain environment, and the alternative outcomes of the decision process. A conceptual foundation such as this is of critical importance because it will *define* fishery management where it has not been heretofore defined. The definition will *enable* all concerned to have an improved perception on "just what fishery management is", but more importantly it will provide a quantitative framework for allocating budgetary funds to various parts of the decision making activity.

Development of the management process needs to be undertaken in the context of a management information system. The information system may be considered as a series of activities. The activities are 1) obtaining bioeconomic data on the operation of the fishery, 2) synthesizing these data into reports or other forms of information, 3) constructing "regulations" based upon the information, 4) executing or implementing the regulations, 5) engaging in enforcement activity and 6) evaluating the entire process (viz, activities 1-5). Figure 1 is a diagram showing a hypothetical time-sequence of events that occur in each activity. It is the task of the manager to identify the various events, to decide upon the human and budgetary resources that will be committed to each, and to schedule each event so that the entire set of activities works in the most cost-effective fashion.

In observing many fishery-management operations, we can note that these management activities are often not well defined and the various events in management occur as *ad hoc* reactions. The reactive mode of management and its lack of definition makes it *difficult* to isolate problems which are recurrent and therefore it is hard to achieve solutions. Because of this management is expensive and does not appear to work well.

Thus, we see the potential of considerable improvement in the management process through designing systems that explicitly involve the six activities outlined above and the events that are components of each activity. These events and activities would naturally need to be responsive to and interacting with the great chance uncertainties that are associated with any fisheries management process. These include, *inter alia*, the year-to-year fluctuations in fish stocks, the collapses and explosions, *and whether* or not a stock that is heavily fished has a propensity to increase in abundance with a reduction in fishing.

While the establishment of the six activities is a relatively easy task, the identification of the events, the analysis of the costs-and-benefits of each, the proper time-placement of each event in its activity, and the coordination among activites is a much more complex task. Fortunately, however, there are a variety of operations research techniques that can facilitate the design of a management information system.

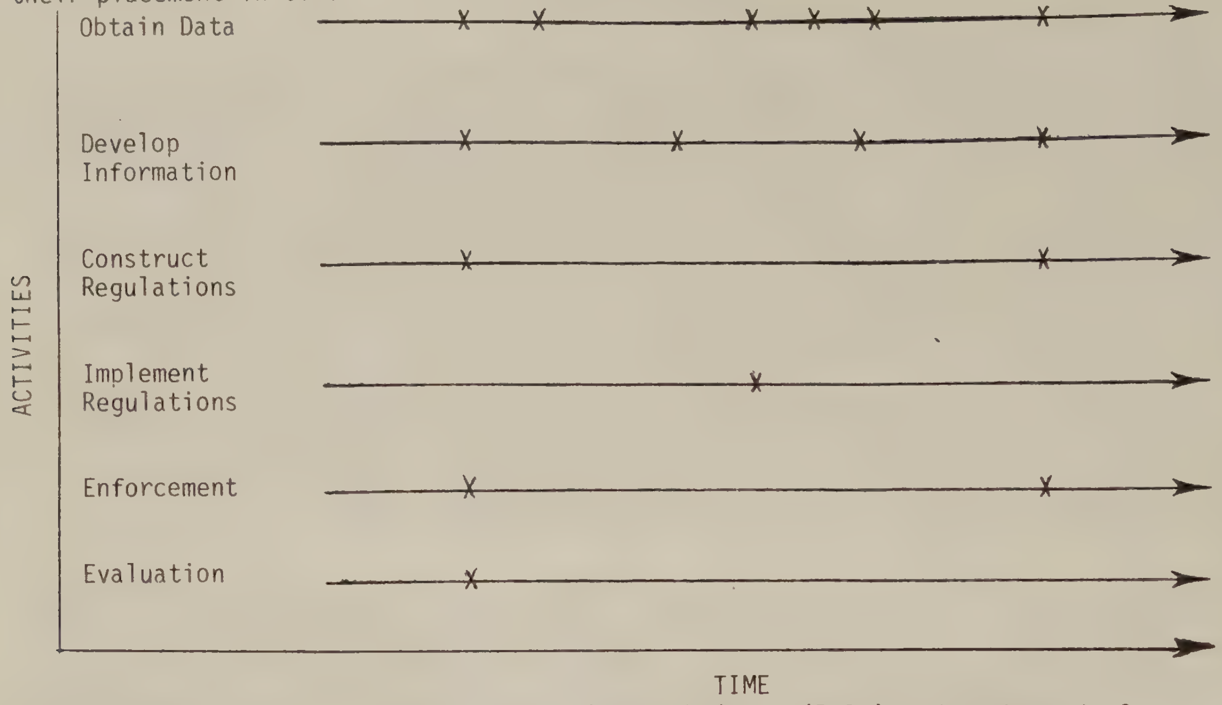


Fig. 1. Six management activities, obtaining data, developing information, constructing regulations, implementing regulations, enforcement and evaluation. The X's refer to hypothetical events in the time stream. Important tasks of management are to identify these events, the magnitude of human and budgetary resources associated with each and their placement in time.

These include program evaluation and review techniques (PERT) and mathematical programming. But there is one technique that seems particularly suitable in the sense that it has a natural relationship to the process of making a sequential decision in time in an uncertain environment. This technique is decision theory.

In this paper we lay a decision-theoretic foundation for the design of a fishery management system. We begin by discussing the fundamental structure of the decision problem taking into account a) chance events, b) decision-making strategies, and c) consequences or payoffs. We then show how these may be employed in various management philosophies (i.e. perfect-knowledge management, maxi-min management, expected-monetary-value management, and expected-utility management. Next, we show how various sampling schemes can improve the management process and give examples which show how comparisons might be made among different management situations such as, prescriptive or adaptive strategies, the timing involved in estimating recruitment, taking into account or ignoring the possibility of catastrophic stock collapses, various sampling distributions and costs for field programs.

FUNDAMENTAL STRUCTURE OF DECISION PROBLEM

As implied earlier the activity of management can be characterized as a series of decisions; decision theory provides a context for analyzing these decisions.

The typical decision problem in its simplest form requires the specification of three components. These are 1) the chance events about which a decision is made, 2) a list of decisions or actions that will be undertaken before observing the chance event and 3) the consequences given the particular chance event and the action that is taken.

A) Chance Events A chance event is an event that occurs as the result of a random or chance process. Examples of chance events are the occurrence of a head in a flip of the coin or drawing an ace from a deck of cards. The most evident chance event in fish-population dynamics is the magnitude of year-class strength. With respect to year-class strength, the chance process may be thought of as being motivated by Nature. In effect Nature selects the size of the year-class, 0, according to some probability distribution. If the decision problem involves a single year, then the outcome of the chance process might be described in terms of a good year class O=G, a poor year class O=P, and a catastrophically poor year class O=C. If, however, the decision problem considers a sequence of years, say N years, then the outcome would be of the form

$$\underline{O} = (O_1 = i, O_2 = i, \ldots, O_n = i)$$

where i = G, P or C (Note that $\underline{O}$ is sometimes called Nature's strategy). The linkages among the O_1's are obviously an important part of the problem. The O_1's may be independent of one another or they may be dependent. The simplest form of dependence would occur if there were a stock-recruitment relationship. Such a relationship would imply that the recruitment in any year would depend upon recruitment in previous years and the amount of fishing in those years.

B) The Decision Makers Strategies The decision maker attempts to guess O in a single year problem or $\underline{O}$ in a multiple year problem. He then undertakes some action or set of actions. This action may be denoted by A for a single year or

$$\underline{A} = (A_1, A_2, \ldots, A_N)$$

for the multiple N-year problem. $\underline{A}$ is frequently called a strategy.

Strategies may involve sampling. In the context of decision analysis, "sampling" refers to undertaking a survey, or a field program, or some other method of acquiring additional information regarding the system with the intent of reducing uncertainty and improving the decision process. It is obvious that if sampling is considered, then its cost and the value of its benefits will be an important part of the analyses.

Strategies may be prescriptive or adaptive. A prescriptive strategy is one in which each year's actions are determined in the first year and an adaptive strategy is one in which each year's actions are determined sequentially each year based upon observations of the stock in that year or in previous years.

For the purpose of this exposition the actions that comprise strategies involve setting the magnitude of fishing mortality in each year. Thus A=H would refer to high fishing mortality, A=L would refer to low fishing mortality and A=Z would refer to zero fishing mortality.

C) Consequences or Payoffs Generally speaking a $\underline{O}$ and $\underline{A}$ (where the number of elements in $\underline{O}$ and $\underline{A}$ may each number from 1 to N) will determine a particular payoff. Payoffs are usually measured in monetary units. Intuitively, it is easy to think that sustained heavy fishing on small year classes would result in low payoffs. An example of an integration of these three components in a decision tree is shown in Figure 2.

Figure 2 shows, for example, that if the year class is good (O=G) and the manager decides to fish heavily, then the payoff will be 25 monetary units. (The payoffs were chosen for demonstration purposes, but are intuitively of the right magnitude).

An important simplifying assumption should be mentioned at this point. That is, if in reality fishery problems were independent single-year problems, then it would be most profitable to catch as much fish as possible. This is of course not really the case since there would be no individuals left to spawn - so the example here is really intended to reflect what would happen with very short lived fish and the payoff includes the maintenance of an appropriate size spawning stock.

THE MANAGEMENT PROCESS

The preceding discussion developed the notion that the decision making process - that is, the process of management - involves listing Nature's strategies, the decision makers strategy, and the payoffs. But how does one select the right action or strategy? In this section we discuss the question of selecting the right action or strategy and how the strategy might be improved by increasing information on nature's strategy through sampling. First the problem is considered as a single-year problem to demonstrate the methodology and then it is considered as a multiple year problem.

Perfect knowledge management

If in fact 0 were known - that is, if it were known in advance whether a year class was G, P, or C, then the correct course of action would be obvious (Figure 2). That is

a) If 0=G, choose H and gain 25 units.

b) If 0=P, choose L and gain 5 units.

c) If 0=C, choose Z and gain -5 units.

Each action would thus, given that 0 is known, maximize the return. But, as it is in the real world of fisheries 0 is never known with certitude. Thus, procedures need to be applied which take into account the uncertainty that is associated with 0.

Maxi-min management (information not available)

If 0 is not known, then one approach to selecting A is to pick that A that results in the greatest minimum value for all possible 0. Choosing this action protects the manager against the worst possible outcome.

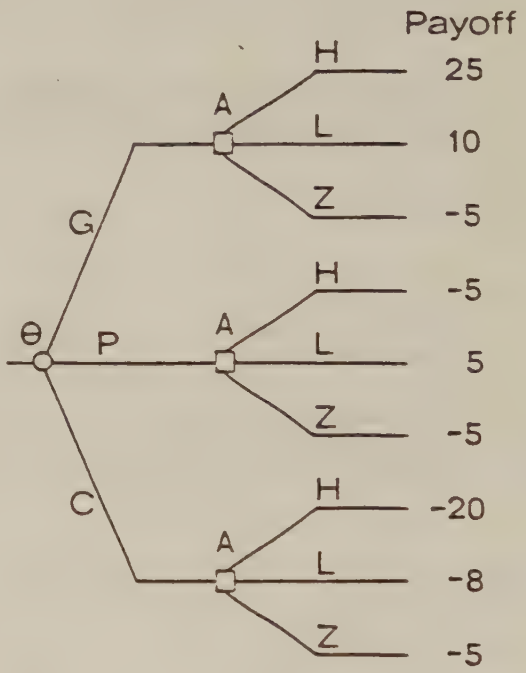


Fig. 2. Example of decision tree showing integration of the chance event, 0, the action or strategy, A, and the payoff in numerical monetary units.

For example, referring to Figure 1, we see that for A=H, heavy fishing, the minimum value is -20; for A=L, the minimum value is -8; and for A=Z, the minimum value is -5. Thus under maxi-min management the action, Z, would be taken and, taking the action Z ensures that whatever 0 is, the maximum loss will be -5.

Expected monetary value (EMV) Management

Intuitively we can see that if we had some idea regarding the probability of each possible outcome of 0, then we ought to be able to do better than we would protecting ourselves against the absolutely worst case as when the maxi-min criterion is used. Suppose we have some means of knowing that 0=C is a relatively rare event and that the possible outcomes have the following probabilities

Pr (0=G) = 0.45

Pr (0=P) = 0.45

Pr (0=C) = 0.10

the weighted average value of each action or the expected monetary value of each action is given by

$$E\ (V|A=H) = .45\ (25) + .45\ (-5) + .10\ (-20) = 7.0$$

$$E\ (V|A=L) = .45\ (10) + .45\ (5) + .10\ (-8) = 5.95$$

$$E\ (V|A=Z) = .45\ (-5) + .45\ (-5) + .10\ (-5) = -5.0$$

Employing the EMV criterion in this case, one would choose the action, H, exerting a maximum amount of fishing effort because this would maximize the average return from fishing.

Expected Utility Management

The result which advises us to maximize fishing effort may seem curious, but it is not. This is because the result contains only part of the information in the decision problem. That is each action may be met with responses of different variability. One measure of this variability is variance about the expected monetary value.

$$\mathrm{Var}\ (V|A=H) = 283.5$$

$$\mathrm{Var}\ (V|A=L) = 27.2$$

$$\mathrm{Var}\ (V|A=Z) = 0$$

One can see that if action H is chosen then the results will be met with high interannual variability. On the other hand if one were to choose action Z the results would not differ from year to year. Thus the manager is faced with the question: Should he pick action H and maximize expected return, but suffer the high probability that in some years he might have disasterous results while in other years he might have very good results or, on the other hand, should he take action L in which he would not make as much on the average, but what he would make would be relatively more certain. Unless he practiced maxi-min management he would not choose Z, because in this particular case a loss of 5.9 units could be guaranteed. The problem now becomes a little more difficult because there is no obvious solution as to whether to choose H with a high EMV and a high uncertainty in payoff or to choose L with a lower EMV which is more certain.

The tradeoff between uncertainty in payoff and expected monetary value is conventionally assessed in terms of utility. The notion of utility is generally referenced to the notion of a lottery. Each lottery is comprised of a series of tickets. Each ticket in the lottery has a certain payoff and a probability of winning associated with it. Suppose you were offered a ticket with a $10 payoff and a 20 percent chance of winning. To break even, on the average, you would expect to pay $2.00 for the ticket. If you pay more for the ticket you are risk prone and if you pay less for the ticket you are risk averse. The utility, U(V), corresponding to a value, V, is the probability of winning the lottery that leaves the decision maker (that is the buyer of the ticket) indifferent between buying the ticket and keeping the value as a certain outcome.

Utility functions can be constructed to represent almost any attitude toward risk. Three general categories of attitude toward risk are risk averse, risk neutral and risk prone. All risk averse utility functions are concave, risk neutral utility functions are straight lines and risk prone utility functions are always convex (Figure 3a). In addition to these general categories, attitudes toward risk can be classified further based on how risk aversion (or proneness) is affected by asset position. Three such classes are constant, increasing and decreasing risk aversion (proneness). All utility functions that describe constant risk aversion are of the form

$$u\ (v) = a - be^{-\gamma V} \quad (1) \qquad \text{(Keeney and Raiffa 1976)}$$

For convenience, we will restrict subsequent discussions on utility to utility functions representing constant risk aversion.

The parameters, a and b, in equation (1) scale the utility function and the parameter β, represents the strength of risk aversion. Larger values of β represent greater aversion to risk and generate more bow-shaped utility functions (Figure 3b). Typically u(V) is scaled to the interval 0,1 such that $u(V_{min})=0$ and $u(V_{max})=1$.

with $V_{min} = -20$
$V_{max} = 25$ (see Figure 2)
and arbitrarily set to .05

$$u(V) = 1.1\ (1-e^{-.05(V+20)})$$

IMPROVING KNOWLEDGE ON NATURE'S STRATEGY

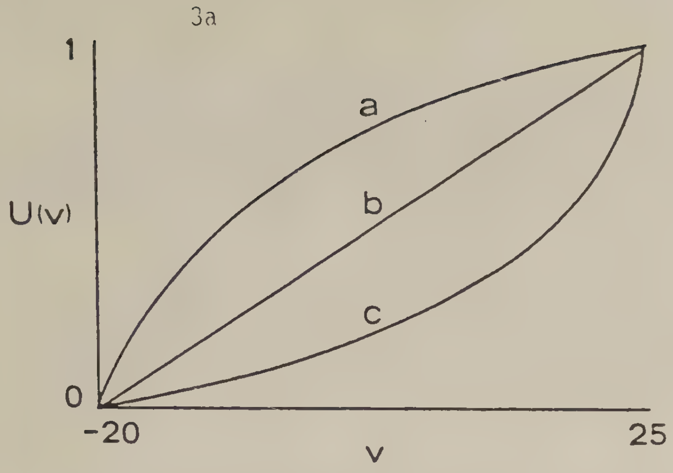
Under perfect-information management, 0 was known and the correct decision could always be made. The perfect-information situation does not exist, but it is useful for comparative purposes. Under maxi-min management, 0 did not have to be known, but the range of payoffs for each action was required. The fact that 0 is not known under maxi-min management results in a very conservative approach. Under EMV management, information on the probability of any particular 0 was required and the utilization of information on 0 enabled a more finely-tuned criterion. The major problem with EMV is that decision makers may vary in their assessment of the worth of a particular EMV; this being particularly true when the variance of any payoff varies with the amount of the payoff. Utility theory accounts for this, but it requires the difficult analysis of attitudes toward risk.

A key question in the EMV or expected utility process involves whether or not information on 0 should be obtained and if it is obtained how precise should this information be. The degree to which 0 is understood is a central issue in improving the performance of management. Mechanisms for understanding 0 are of considerable practical importance because they may involve complicated long-term research or extensive at-sea sampling programs.

Deciding on how to investigate 0 is not generally a simple problem that a large element in improving the performance of management is to increase our knowledge of 0. There are in most instances numerous approaches to increasing knowledge about 0. While knowledge on 0 generally can be increased at some cost, not all increases in knowledge on 0 will be cost effective.

Perhaps, the simplest way of estimating 0 is to assume that causal factors have remained stable over the years and hence use past information to estimate 0 for the future. Par exemplo, suppose a fishery was observed for twenty years and there were 10 G year classes, 8 P year classes and 2 C year classes. The following estimates could be made; Pr (0=G) = 10/20, Pr (0=P) = 8/20, Pr (0=C) = 2/20. However, an assumption implicit in the above procedure is that the underlying mechanisms which cause large and small year classes is the same year-in-and-year-out. That is, in the future, Pr (0=G) is very close to 10/20; Pr (0=P) is very close to 8/20 and Pr (0=C) is very close to 2/20. To the intuition, it seems unlikely that conditions will stay the same for a number of years and hence it is desirable to collect and employ additional information.

The notion that conditions stay the same over years implies that there would be no discernable time trend in recruitment. Hence, the recruitment that would be predicted each year, is just the average recruitment and the variability associated with that prediction would be relatively large. This variability could be reduced if it were known that there was some independent variable or set of independent variables which recruitment would depend upon. This one would still need to assume that the relationship between recruitment and the independent variables would need to be the same. If as we suspect this relationship changes or the set of variables changes then the quality of the predictions could substantially deteriorate.



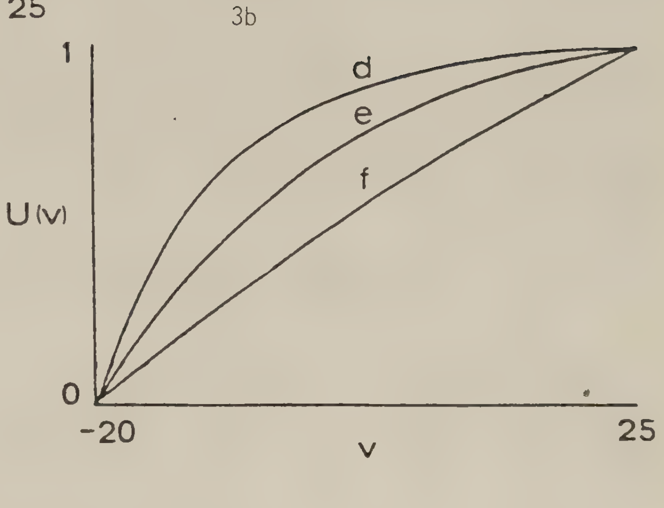
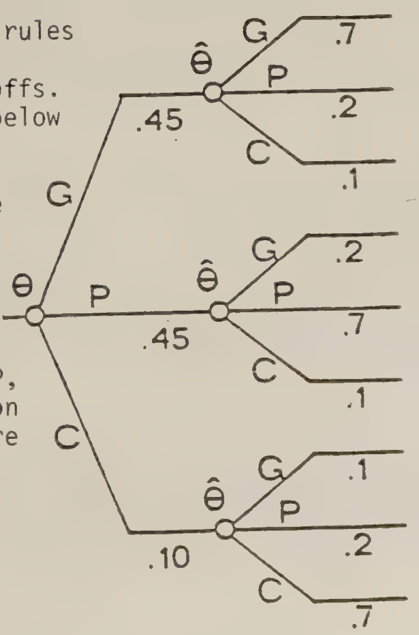


Fig. 3. Hypothetical utility functions. The ranking of actions based on expected utility, E[u(v)], depends on the shape of the utility function - both the general class of function and particular parameters affect that shape. The curves in Figure 3a are examples of risk averse (a) risk neutral (b) and risk prone (c) utility functions. The curves in Figure 3b are all constant risk averse utility functions: [illegible] =1 in d, [illegible] =.01 in f and [illegible] =.05 in e (the example discussed in the text).

Fig. 4.
A decision tree depicting the affect of sampling and associated decision rules on the probability distribution of payoffs. The decimal number below each branch is the probability of the corresponding chance event. For example, Pr (0=C)=.1 and Pr (0̂=P|0=C)=.2, therefore the joint probability for the history, 0=C and 0̂=P, is .02. The decision rules represented are if 0̂=G then A=H, if 0̂=P then A=L and if 0̂=C then A=Z.



$\Pr[\hat{\theta}=\hat{\theta}_i \mid \theta=\theta_j] \times \Pr[\theta=\theta_j]$	Action	Payoff
.315	H	25
.09	L	10
.045	Z	-5
.09	H	-5
.315	L	5
.045	Z	-5
.01	H	-20
.02	L	-8
.07	Z	-5

The question of acquiring additonal information and assessing its value can be determined using decision theory, the use of which is facilitated by a decision tree. Figure 4 shows a decision tree which would be characteristic of the fisheries management process. The particular tree shown in the figure gives the basic elements: Nature selects 0, a scientific program samples the system to guess 0, the manager makes a decision and then nature selects another 0.

Obviously, the manager will want to improve his ability to guess 0. Therefore, he should want his probability of detecting the true 0, i.e. $Pr(\hat{0}=\hat{0}_i | 0=0_i)$ to be high and the probability of making a mistake, $Pr(\hat{0}=\hat{0}_i | 0=0_j)$, $i \neq j$ to be low. However, the value of the estimation process depends on how the estimates affect the choice of an action as well as how good the estimates are.

Suppose the decision rules are if $\hat{0}_t= G$ do $A_t= H$; if $\hat{0}_t= P$ do $A_t= L$; and if $\hat{0}_t=C$ do $A_t=Z$ (Figure 4). The EMV for this combination of estimation and choice is 8.74. The best that could be done with the same probabilities for 0 but no sampling was an EMV = 7 for A=H. So that sampling scheme would result in an expected increase of 1.74 in the EMV over a program where sampling is not utilized. A similar analysis could be made for expected utility.

THE PROBLEM OF TIME AND MULTIPLE YEAR DECISION ANALYSIS

A time horizon is a point in time beyond which the benefits of planning do not excede the costs, usually because of uncertainty into the future. While time horizons in fisheries may not be long, they are probably longer than one year in most instances and hence it is important to consider multiple year decision analysis.

Multiple year decision analysis requires considering simultaneously the set of 0's, one for each year and the set of possible actions that might arise in response to a particular set of 0's.

The linkage among 0's can be represented by transition probabilities $Pr(0_t | 0_{t-1}, A_{t-1}, 0_{t-2}, A_{t-2}, \ldots)$. For the purpose of this elementary exposition we only consider probabilities of the form $Pr(0_t \; 0_{t-1}, A_{t-1})$ which relate recruitment in year t with the recruitment and the action in year t-1.

In order to demonstrate the procedure we have contrived three stock recruitment hypotheses (Table 1). H_1 represents no relationship between stock and recruitment and no chance of a catastrophic decline. H_2 represents a positive monotonic stock and recruitment relationship with no chance of a catastrophic decline and H_3 represents a monotonic stock and recruitment relationship with a small chance of a catastrophic decline.

In a multiple year setting the multiple-actions can also be linked together. Each set of multiple actions is called a strategy (for example a four year strategy would be (A_1, A_2, A_3, A_4). There are two approaches to linking the strategies together.

The first approach is prescriptive. In other words the alternative strategies are decided before the management routine is implemented. For example, within a three year time horizon it would be decided to engage in heavy fishing each year so $\underline{A}$ = (H, H, H). Table 2 gives two examples of a prescriptive strategy.

The second approach is adaptive. In this second approach the action in any year depends upon sampling the system to improve the guess of 0. So an adaptive strategy requires specification of 1) the sampling procedure, 2) the method of estimation and 3) the decision rule which will give the alternative action based upon the estimate. Tables 3-10 give examples of adaptive strategies.

Hypothesis	θ_{t-1}	A_{t-1}	$Pr\ (\theta_t \mid \theta_{t-1}\ \&\ A_{t-1})$		
			θ_t		
			G	P	C
1	G	H	.50	.50	.00
		L	.50	.50	.00
		Z	.50	.50	.00
	P	H	.50	.50	.00
		L	.50	.50	.00
		Z	.50	.50	.00
	C	H	.00	.00	.00
		L	.00	.00	.00
		Z	.00	.00	.00
2	G	H	.60	.40	.00
		L	.70	.30	.00
		Z	.80	.20	.00
	P	H	.20	.80	.00
		L	.30	.70	.00
		Z	.40	.60	.00
	C	H	.00	.00	.00
		L	.00	.00	.00
		Z	.00	.00	.00
3	G	H	.60	.38	.02
		L	.70	.28	.02
		Z	.80	.18	.02
	P	H	.15	.80	.05
		L	.25	.70	.05
		Z	.35	.60	.05
	C	H	.02	.08	.90
		L	.02	.18	.80
		Z	.02	.28	.70

Table 1: Three stock-recruitment hypotheses represented by transition probabilities. Each entry for each hypothesis is the probability that O_t=i given that O_{t-1}=j and A_{t-1}=k (where i=G, P or C; j=G, P or C and k=H, L or Z).

Strategy	t (year)	A_t
1	1	H
	2	H
	3	H
2	1	L
	2	L
	3	L

Table 2: Two prescriptive strategies for a three year time horizon. Strategy 1 specifies heavy fishing in each year and strategy 2 specifies a low level of fishing in each year.

Table 3: An adaptive strategy specified by decision rules, 3a, and a sampling distribution of $\hat{0}_t$, 3b. Entries in the right hand column of 3a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 3b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

3a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t \& \hat{\theta}_{t-1}$
3	G	G	H
		P	L
	P	G	H
		P	L

3b

Strategy	θ_t	A_t	$\Pr(\hat{\theta}_t \mid \theta_t \& A_t)$		
			$\hat{\theta}_t$		
			G	P	C
3	G	H	.70	.30	.00
		L	.60	.40	.00
		Z	.00	.00	.00
	P	H	.30	.70	.00
		L	.40	.60	.00
		Z	.00	.00	.00
	C	H	.10	.90	.00
		L	.20	.80	.00
		Z	.00	.00	.00

4a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t \& \hat{\theta}_{t-1}$
4	G	G	H
		P	L
	P	G	H
		P	L

4b

Strategy	θ_t	A_t	$Pr(\hat{\theta}_t \mid \theta_t \& A_t)$		
			$\hat{\theta}_t$		
			G	P	C
4	G	H	.90	.10	.00
		L	.80	.20	.00
		Z	.00	.00	.00
	P	H	.10	.90	.00
		L	.20	.80	.00
		Z	.00	.00	.00
	C	H	.05	.95	.00
		L	.10	.90	.00
		Z	.00	.00	.00

Table 4: An adaptive strategy specified by decision rules, 4a, and a sampling distribution of $\hat{0}_t$, 4b. Entries in the right hand column of 4a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 4b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

5a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t \& \hat{\theta}_{t-1}$
5	G	G	H
		P	L
		C	Z
	P	G	H
		P	L
		C	Z
	C	G	H
		P	L
		C	Z

5b

Strategy	θ_t	A_t	$Pr(\hat{\theta}_t \mid \theta_t \& A_t)$		
			$\hat{\theta}_t$		
			G	P	C
5	G	H	.70	.28	.02
		L	.60	.37	.03
		Z	.55	.40	.05
	P	H	.30	.65	.05
		L	.40	.53	.07
		Z	.45	.45	.10
	C	H	.10	.20	.70
		L	.20	.25	.55
		Z	.25	.25	.50

Table 5: An adaptive strategy specified by decision rules, 5a, and a sampling distribution of $\hat{0}_t$, 5b. Entries in the right hand column of 5a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 5b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

6a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t$ & $\hat{\theta}_{t-1}$
6	G	G	H
		P	L
		C	Z
	P	G	H
		P	L
		C	Z
	C	G	H
		P	L
		C	Z

6b

Strategy	θ_t	A_t	$\Pr(\hat{\theta}_t \mid \theta_t$ & $A_t)$		
			$\hat{\theta}_t$		
			G	P	C
6	G	H	.90	.09	.01
		L	.80	.18	.02
		Z	.60	.36	.04
	P	H	.10	.88	.02
		L	.20	.75	.05
		Z	.40	.53	.07
	C	H	.05	.10	.85
		L	.10	.20	.70
		Z	.20	.20	.60

Table 6: An adaptive strategy specified by decision rules, 6a, and a sampling distribution of $\hat{0}_t$, 6b. Entries in the right hand column of 6a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 6b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t$ & $\hat{\theta}_{t-1}$
7	G	G	H
		P	H
	P	G	L
		P	L

7a

Strategy	θ_t	A_t	$\Pr(\hat{\theta}_t \mid \theta_t$ & $A_t)$		
			$\hat{\theta}_t$		
			G	P	C
7	G	H	.70	.30	.00
		L	.70	.30	.00
		Z	.00	.00	.00
	P	H	.30	.70	.00
		L	.30	.70	.00
		Z	.00	.00	.00
	C	H	.10	.90	.00
		L	.10	.90	.00
		Z	.00	.00	.00

7b

Table 7: An adaptive strategy specified by decision rules, 7a, and a sampling distribution of $\hat{0}_t$, 7b. Entries in the right hand column of 7a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 7b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

8a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t \& \hat{\theta}_{t-1}$
8	G	G	H
		P	H
	P	G	L
		P	L

8b

Strategy	θ_t	A_t	$Pr(\hat{\theta}_t \mid \theta_t \& A_t)$		
			$\hat{\theta}_t$		
			G	P	C
8	G	H	.90	.10	.00
		L	.90	.10	.00
		Z	.00	.00	.00
	P	H	.10	.90	.00
		L	.10	.90	.00
		Z	.00	.00	.00
	C	H	.05	.95	.00
		L	.05	.95	.00
		Z	.00	.00	.00

Table 8: An adaptive strategy specified by decision rules, 8a, a sampling distribution of $\hat{0}_t$, 8b. Entries in the right hand column of 8a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 8b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t \& \hat{\theta}_{t-1}$
9	G	G	H
		P	H
		C	H
	P	G	L
		P	L
		C	L
	C	G	Z
		P	Z
		C	Z

9a

Strategy	θ_t	A_t	$Pr(\hat{\theta}_t \mid \theta_t \& A_t)$		
			$\hat{\theta}_t$		
			G	P	C
9	G	H	.70	.28	.02
		L	.70	.28	.02
		Z	.70	.28	.02
	P	H	.30	.65	.05
		L	.30	.65	.05
		Z	.30	.65	.05
	C	H	.10	.20	.70
		L	.10	.20	.70
		Z	.10	.20	.70

9b

Table 9: An adaptive strategy specified by decision rules, 9a, and a sampling distribution of $\hat{0}_t$, 9b. Entries in the right hand column of 9a are the action to be taken in year t given the estimates of 0 in years t and t-1. Entries in 9b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

10a

Strategy	$\hat{\theta}_t$	$\hat{\theta}_{t-1}$	$A_t \mid \hat{\theta}_t$ & $\hat{\theta}_{t-1}$
10	G	G	H
		P	H
		C	H
	P	G	L
		P	L
		C	L
	C	G	Z
		P	Z
		C	Z

10b

Strategy	θ_t	A_t	Pr ($\hat{\theta}_t \mid \theta_t$ & A_t)		
			$\hat{\theta}_t$		
			G	P	C
10	G	H	.90	.09	.01
		L	.90	.09	.01
		Z	.90	.09	.01
	P	H	.10	.88	.02
		L	.10	.88	.02
		Z	.10	.88	.02
	C	H	.05	.10	.85
		L	.05	.10	.85
		Z	.05	.10	.85

Table 10: An adaptive strategy specified by decision rules, 10a, and a sampling distribution of $\hat{0}_t$, 10b. Entries in the right hand column of 10a are the actions to be taken in year t given the estimates of 0 in years t and t-1. Entries in 10b are the probabilities that the estimate, $\hat{0}_t$, will be G, P or C given 0 and A in year t.

Table 11: Summary of the characteristics and expected payoff, EMV (in units of net present value), for ten hypothetical strategies under each of three stock-recruitment hypotheses (see Table 1). These expected payoffs were computed for a three year time horizon with a 10% annual discount rate. The payoff in each year, given a particular O and A, was the same as for the one year example (see Figure 2).

						EMV (as net present value)		
						S-R Hypothesis		
	Characteristics of Strategy					1	2	3
Strategy	Prescriptive (P) or Adaptive (A)	Timing of Estimate of θ	Allows for Catastrophic Recruitment	Sampling Intensity	Relative Cost	No Catastrophes No S-R Relationship	No Catastrophes S-R Relationship	Catastrophes S-R Relationship
1	P	-	-		0	27	8	-1
2	P	-			0	21	18	15
3	A	t-1	no	low	1	20	16	11
4	A	t-1	no	high	2	17	15	10
5	A	t-1	yes	low	1	19	15	10
6	A	t-1	yes	high	2	17	14	9
7	A	t	no	low	2	25	15	10
8	A	t	no	high	3	29	19	13
9	A	t	yes	low	2	24	14	9
10	A	t	yes	high	3	29	19	14

Information on the sampling procedure and the estimation method is contained in the conditional sampling distribution of the estimate $\hat{O}_t$, V_{iz}, $Pr\ (\hat{O}_t | O_t, A_t)$. Further, the decision rules may depend upon $\hat{O}_t$, and $\hat{O}_{t-1}$, V_{iz}, $A_t = f\ (\hat{O}_t, \hat{O}_{t-1})$. To show the possibilities of these analyses, the results are shown in Table 11 and from the Table we can see that the decision maker has many options and approaches which he can use to structure the management process. While the results are presented in terms of EMV it should be easy to see that they can be presented in terms of utility as well.

DISCUSSION

There is a growing perception that traditional fisheries management does not work as well. It appears to be inefficient. That is, social and economic benefits produced as a result of management are not sufficient to warrant costs, and management schemes are often associated with political strife and contention.

Various causes have been ascribed to this malaise. For example the "open-access" regime was thought to be a major obstacle preventing efficient and contention-free management. While the importance of the nature of access cannot be denied, it is now generally thought that the key constraint toward effective management is the inefficient way in which governments exert their management authorities.

The problem is quite complex. The critical difficulty is of course to change the socio-economic conditions that foster poor management. Many believe though that an improvement in our understanding of fishery dynamics will be a prerequisite to improving the socio-economic conditions. On the other hand without improvement in these conditions it will be difficult to obtain the resources to improve our understanding of fishery dynamics.

This dilemma is further strengthened because managers are constrained by traditional models. The traditional production-model, yield-per-recruit, and stock and recruitment approaches produce results which are only useful for the "average year" and do not provide needed guidance for year-to-year strategies. Extraordinarily large and small year classes occur typically and the conventional management algorithms are not structured to account for these aberrancies. Further the ultimate goals of management are generally economic in nature and yet the deficiencies in biological models are certainly no worse than the deficiencies in economic models, particularly those of estimating supply curves. It is obvious that the development of new models is not just a mathematical exercise, but rather it is an exercise in obtaining new data and information which can be used to structure and formulate the new models.

Since the traditional models cannot predict more than, "on the average events", generally based upon past environmental conditions, the nature of which are generally not understood, the critical problems of stock collapse, effects of environmental modification, and stock rebuilding are addressed only superficially.

It appears that one major constraint in solving these problems is the optimal allocation of budgetary and human resources to each management activity. Obviously the most efficient approach for allocating resources to the various components of management is to examine management process in its entirety, taking into account the special problems of management under uncertainty. An examination and analysis of the entire process will reveal those elements that are relatively important and those that need special attention.

The beauty of the decision-theory approach is that it enables such a "first-cut comparison" (i.e. magnitude of the costs and benefits) of various management structures (e.g. timing of management activities, hypotheses on population dynamics, and sampling schemes) for different management philosophies (e.g. EMV and expected utility) for various probability structures (i.e. varying degrees of entropy).

The first cut comparison can then be used to initialize iterative improvement of the management activities posed in Figure 1.

It is easy to see that in addition to formalizing the structure the decision theory approach requires a particular examination of 1) states of Nature, 2) alternative actions, 3) various metrics of performance such as catch or economic values, 4) discount rates, 5) utility functions, 6) hypotheses on population dynamics including those on stock-and-recruitment, 7) and the identification of appropriate planning horizons.

Thus to address technical issues of management we must consider management as an entity in its own right. More specifically, the task of fishery managers involves the design of fishery management systems. The ten strategies articulated in this paper are in fact rudimentary fishery management systems which can be applied in real world fisheries, not only for management in the more narrow sense, but for management in the broader sense where the kinds and quality of information are carefully specified.

ACKNOWLEDGEMENTS

This paper was motivated by my (BJR) study of the Namibian pilchard fishery. I am indebted to John Gulland for his assistance.

REFERENCES

FAO. 1980. Report of the ACMRR Working Party on the Scientific Basis of Determining Management Measures. Rome, 1980. FAO Fish.Rep. (236):149 p.

Keeney, R.L. and H. Raiffa. 1976. Decisions with Multiple Objectives: Preferences and Value Tradeoffs. John Wiley and Sons, New York. 569 p.

APPLICATION OF A LAEVASTU-LARKINS ECOSYSTEM MODEL FOR BERING SEA GROUNDFISH MANAGEMENT

by

Loh-Lee Low

Northwest and Alaska Fisheries Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2725 Montlake Boulevard East
Seattle, Washington 98112
USA

Resumen

En la evaluación y ordenación de los recursos de especies de fondo del Mar de Bering se ha dado un gran valor práctico al uso de modelos de ecosistemas como medio para mejorar el análisis tradicional por especies de los datos de la pesquería. En este trabajo se muestra que el modelo de Laevastu-Larkins, el modelo PROBUB, puede ser utilizado para evaluar las tendencias a largo tiempo de los niveles de población de los varios grupos de peces de fondo y que su uso puede determinar cambios en el establecimiento de las regulaciones de cuotas de captura. El uso del modelo ha dado por resultado que al establecer cuotas de capturas se tomen en consideración aspectos que son diferentes de aquéllos provenientes de estimados basados en análisis mono-específicos de cuatro grupos de especies. El modelo sugiere que puede ser poco realísta tratar de reconstruir dos stocks a sus niveles altos debido a que los niveles bajos actuales corresponden al nivel normal a largo tiempo. El modelo también ha mostrado que las comunidades de peces de fondo fluctuan en promedio en un 22% en un ciclo de cinco a seis años. La mayor fluctuación para una de las especies componentes es tan alta como el 50% en tres años. Todos los otros grupos de especies, a excepción del grupo de peces de rocas de vida larga, muestran fluctuaciones del 8 al 30% en ciclos de cinco a diez años. El modelo sin embargo no puede todavía remplazar los métodos de análisis tradicional mono-específicos para la ordenación de la pesquería, ya que estos análisis proporcionan un gran número de detalles esenciales sobre los cambios de año a año en la tendencia general, en la composición por especies, la estructura por edades, y la característica de la dinámica de población de cada stock.

INTRODUCTION

Large variations in production of neritic fish resources have been well illustrated throughout this meeting. Similar variations, perhaps of smaller amplitude and notoriety, occur commonly in the demersal and semi-demersal fisheries resources as well. A case to be illustrated here is the Bering Sea groundfish resource. Over the past thirty years, catches of groundfish have fluctuated through several distinct cycles (Bakkala et al., 1979). A peak catch of 750,000 t in 1961 dominated by yellowfin sole *Limanda aspera* was attained in the first obvious cycle (Figure 1). This was followed by a record catch of 2.2 million t in 1972 when the dominant species had switched to walleye pollock *Theragra chalcogramma*. Since 1977, catches have varied in a relatively narrower range between 1.2 and 1.4 million t, largely as a result of imposed catch quotas. The quotas stabilized catches that would otherwise follow wide natural fluctuations in abundance of the stocks.

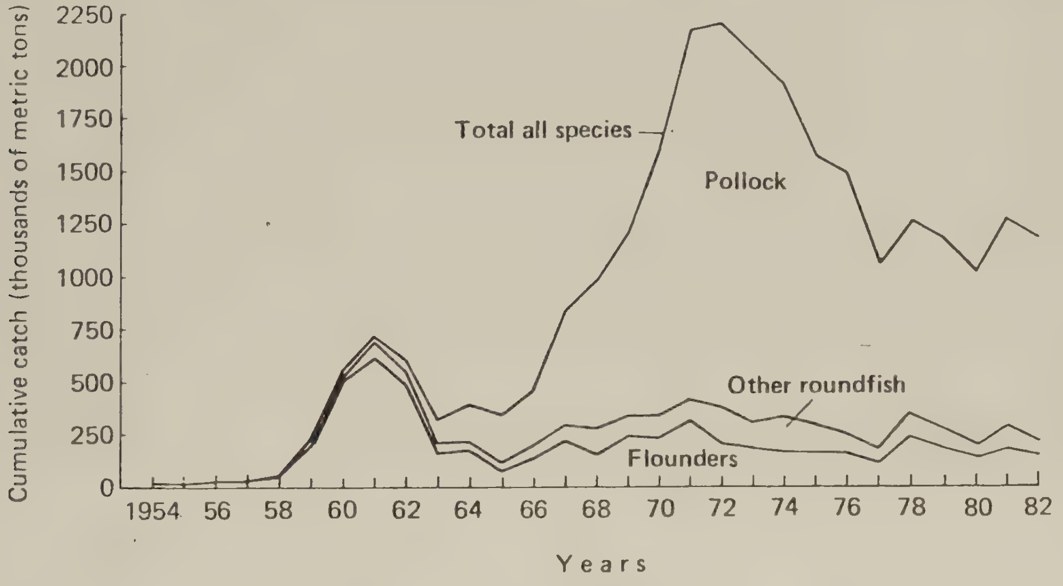


Figure 1. Groundfish catches in the Bering Sea, 1954-82.

General major causes for such natural variations in the production of groundfish in the Bering Sea have been discussed by Laevastu et al. (1982). They noted that besides external factors, such as effects of temperature anomalies and fishing; ecosystem internal factors like predation, cannibalism, competition, and migration can contribute significantly to the fluctuations of population biomass.

More specific year-to-year variations can be illustrated from status of stocks assessments made on a species-by-species basis as typically reported in Bakkala and Low (1982)1/. These assessments depend largely on single species analytical techniques like empirical evaluations of catch-per-unit-effort trends, and the more sophisticated population dynamics analyses of the data. They provide estimates of potential yield from the resources that largely reflect current and short-term trends, but lack the longer-term effects of fisheries exploitation from an ecosystem context.

This paper will illustrate the use of an ecosystem model developed at the Northwest and Alaska Fisheries Center in Seattle by Dr. Taivo Laevastu (Laevastu and Larkins, 1981) to evaluate some of these effects of fisheries exploitation. The model has been used to supplement traditional species-by-species assessments and its results have led to alternative considerations for catch quotas that are derived through single species analyses of the Bering Sea groundfish resources.

1/ Bakkala, R.G., and L.L. Low (eds.). 1982. Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1982. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., 2725 Montlake Blvd. E., Seattle, WA 98112. (Doc submitted to the Intl. North Pacific Fish. Comm. in Oct. 1982).

STOCK ASSESSMENT AND MANAGEMENT

Although the Bering Sea groundfish fishery is largely a trawl fishery and is multispecies in character, assessment and management of the resources have been approached on a species-by-species basis. The status of individual stocks have been determined for each species or species group and an optimum yield (OY) set for each unit. These OY's eventually become annual catch quotas for management. When the catch quota for a species is reached, the entire fishery or that of a particular group may be subject to closure, even though abundance of the species may have changed to dictate otherwise from the time the quota was set a year or two earlier. This management process under the present fishery management plan (FM Plan) does not, therefore, allow a quick change of the regulations. Instead, the FM Plan requires a lengthy and elaborate review process for a proposed change to be made.

In order to improve on this management system, an amendment to the FM Plan has been developed to manage the groundfish complex as a unit while allowing adjustments to the catch of individual species according to fluctuations in their abundance. The amendment allows the annual OY of the groundfish complex to be set within a 1.4 to 2.0 million t range at the beginning of each year without a lengthy amendment process each time. The OY range has been set to reflect the present yield potential of the resource and the current socio-economic preference of the fishing industry and management to harvest at that range. At the time annual OY is set, catch quotas for the individual component species within the complex are also set to reflect their current status of stocks.

The latest status of stocks analyses reported by Bakkala and Low (1982) 1/ show that the annual surplus production (ASP) of the individual species groups add up to more than 2 million t (Table 1). The term ASP is defined as the annual yield that may be taken without changing the biomass of the stock the following year. The estimates, therefore, reflect the current and short term yield from the resources.

Table 1. Estimated annual surplus production for 1983 and abundance trends for the major commercial groundfish species in the Bering Sea

Species group	Annual surplus production (1,000 t)	Abundance trend
Pollock	1,300.0	Average abundance, on declining trend
Pacific cod	298.0	Historic high abundance, expected to decline rapidly
Yellowfin sole	200.0	Historic high abundance, stable
Turbots	85.0	Average abundance, stable
Other flatfish	120.0	Average abundance, stable
Sablefish	2.9	Low abundance, stable
Other rockfish	14.1	Average abundance, stable
Atka mackerel	26.0	Average abundance, stable
Total groundfish	2,057.8	High abundance, expected to decline slightly

Pollock is clearly the most dominant and productive species in the goundfish complex. Its ASP of 1.3 million t for 1983 accounts for 63% of the total production. The ASP for Pacific cod *Gadus macrocephalus* is next highest (298,00 t) due to the presence of unusually strong year classes and accounts for 15% of the goundfish production. Yellowfin sole production is a close third at 200,000 t, or 10% of total production. The rest of the flatfishes (turbots and other flatfish) account for an ASP of 205,000 t, or another 10% of total production. The turbot group is made up of arrowtooth flounder *Atheresthes stomias* and Greenland turbot *Reinhardtius hippoglossoides*. The other flatfish group is mainly made up of Alaska plaice *Pleuronectes quadrituberculatus*, rock sole *Lepidopsetta bilineata*, and flathead sole *Hippoglossoides elassadon*. The rest of the species--Pacific ocean perch *Sebastes alutus*, other rockfishes *Sebastes* spp, and *Sebastolobus* spp., sablefish *Anaplopoma fimbria*, and Atka mackerel *Pleurogrammus monopterygius* --account for the remaining 2% of the total groundfish production.

Normally, the species-by-species analyses on the status of stocks and ASP's summarized in Table 1 are sufficient basis for setting catch quotas. However, since ecosystem models have been developed to the extent that they can now be used to evaluate long term trends of the groundfish complex, they have been applied to supplement the species-by-species analyses for stock assessment and management.

ECOSYSTEM ANALYSIS

Various computer simulation models have been developed to describe the interrelationship and dynamics of the Bering Sea ecosystem. Two widely tested models are the Prognostic Bulk Biomass (PROBUB) and the Dynamical Numerical Marine Ecosystem (DYNUMES) models developed at the Northwest and Alaska Fisheries Center and described by Laevastu and Larkins (1981). Both models compute the transfer of biomass between trophic levels given natural and man-induced processes that occur in the ecosystem. The PROBUB model is a more detailed representation of its dynamics. To evaluate the long-term consequences of harvesting in this paper, the PROBUB model was used because of its greater simplicity over the DYNUMES model.

PROBUB simulates the dynamics of the ecological components (marine birds, marine mammals, groundfish, pelagic fish, and benthic organisms) and the principal individual species within these components. The model takes into account the biomass of each species group, the prey-predator relationships among these groups and tracks their change in biomass in specific areas and time steps. The input data required to initiate the simulations were described by Laevastu et al. (1980) 2/. These input data are abundance of each species group, their food requirements in terms of species and quantities, and the effects of growth and mortality on the biomass and distribution of species groups.

Several series of simulations were made to evaluate the natural equilibrium and effects of fishing on the ecosystem. There were three series of basic simulations which provided the long-term equilibrium bounds for the populations.

Equilibrium Biomass

Starting with the present species make-up and their prey-predator relationships. PROBUB was run until the species composition (with emphasis on the groundfish species) reached equilibrium. These simulations produce three sets of equilibrium biomass for the various fish groups:

(a) A minimum equilibrium biomass using the lowest estimated food requirements and the highest estimated growth rates of predators,

(b) A maximum equilibrium biomass using the highest estimated food requirements and lowest estimated growth rates of predators, and

(e) The mean equilibrium biomass using the most likely mean values for both requirements.

The estimated levels of minimum and maximum equilibrium biomass for the groundfish groups are shown in Table 2. These equilibria provide the lower and upper bound by which expected long-term effects of fishing can be gauged. The minimum equilibrium biomass for the major species taken in the commercial fishery totals about 19 million t. The maximum is about 32 million t, indicating a long-term average variation of about 13 million t.

On a long term basis, and given the present species composition in the ecosystem, pollock is by far the most abundant and makes up 63% of the total biomass of the groundfish complex. Atka mackerel is the next most abundant species, making up about 9-13% of the biomass. Pacific cod is third and is followed closely by yellowfin sole. Each species makes up about 5-6% of the groundfish biomass. The rest of the species groups make up the remaining 18-20%.

2/ Laevastu, T., P. Livingston, and K. Niggol. 1980. Basic inputs to PROBUB model of the eastern Bering Sea and western Gulf of Alaska. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., 2725 Montlake Blvd. E., Seattle, WA 98112.

Table 2. -- Estimated minimum equilibrium biomass of the major commercially important groundfish species in the Bering Sea by the PROBUB ecosystem model

Species group	Minimum biomass (1,000 t)	Maximum biomass (1,000 t)
Pollack	10,600	20,000
Pacific cod	1,160	1,700
Yellowfin sole	980	1,480
Turbots	540	765
Other flatfish	1,785	2,450
Sablefish	140	200
Pacific Ocean perch	420	720
Other rockfish	980	1,680
Atka mackerel	2,400	2,800
Total Groundfish	19,005	31,795

Experimental Simulations

After the ecosystem model has been simulated to reach the mean equilibrium state, experimental catch levels, equal to or close to ASP's, were incorporated into the simulations to determine their effects on groundfish biomass. As examples, three series of catch levels were simulated (Table 3). These series of catch levels correspond to first-guess acceptable catch estimates used by Laevastu and Larkins (1981). Series A depicts catch and discard levels in 1980. Series B and C depict alternative catch levels that were selected as possible catch quotas. It is obvious that virtually limitless combinations of catches may be simulated and the proper combination would have to be specifically picked. The model computes the changes to the biomass of each species group given the assumption that from the point of mean equilibrium, the fishery will take a constant catch of each species each year as depicted in Series A to C.

Table 3.--Three series of catch levels selected for simulation by the PROBUB ecosystem model

Species group	Catch levels in thousand t		
	Series A	Series B	Series C
Pollock	1,500	1,560	1,135
Pacific cod	100	88	137
Yellowfin sole	86	120	137
Turbots	34	53	53
Other flatfish	66	86	105
Sablefish	9	9	9
Pacific ocean perch	9	9	9
Other rockfish	19	17	19
Atka mackerel	28	47	28
Total groundfish	1,851	1,989	1,632

The 10-year trend of the biomass level resulting from the simulations for each groundfish species and the entire groundfish complex are shown in Figures 2-11. The figures show the minimum and maximum equilibrium biomass for each species, the estimated ASP level for 1983 and how the biomass of each species would change if the resources are exploited at the three series of catch levels.

The manner in which the biomass fluctuates about the minimum and maximum equilibrium bounds may be used to evaluate whether a catch level is appropriate and likely to be sustained. Since the PROBUB model is structured to simulate the long-term average condition of the ecosystem, results shown in Figures 2-11 do not account for short-term anomalies which may cause unusually high or low recruitment levels. Interpretation of these figures should, therefore, take into account these anomalous factors and other population dynamics characteristics of the current populations. These short-term features are more readily revealed by single-species analyses.

In practice, therefore, catch quota regulations for groundfish resources in the Bering Sea have been determined largely from the species-by-species analyses depicted in Table 1, but modified by the longer term simulations depicted in Figures 2-11. A species-by-species interpretation of the figures and pertinent comments follows.

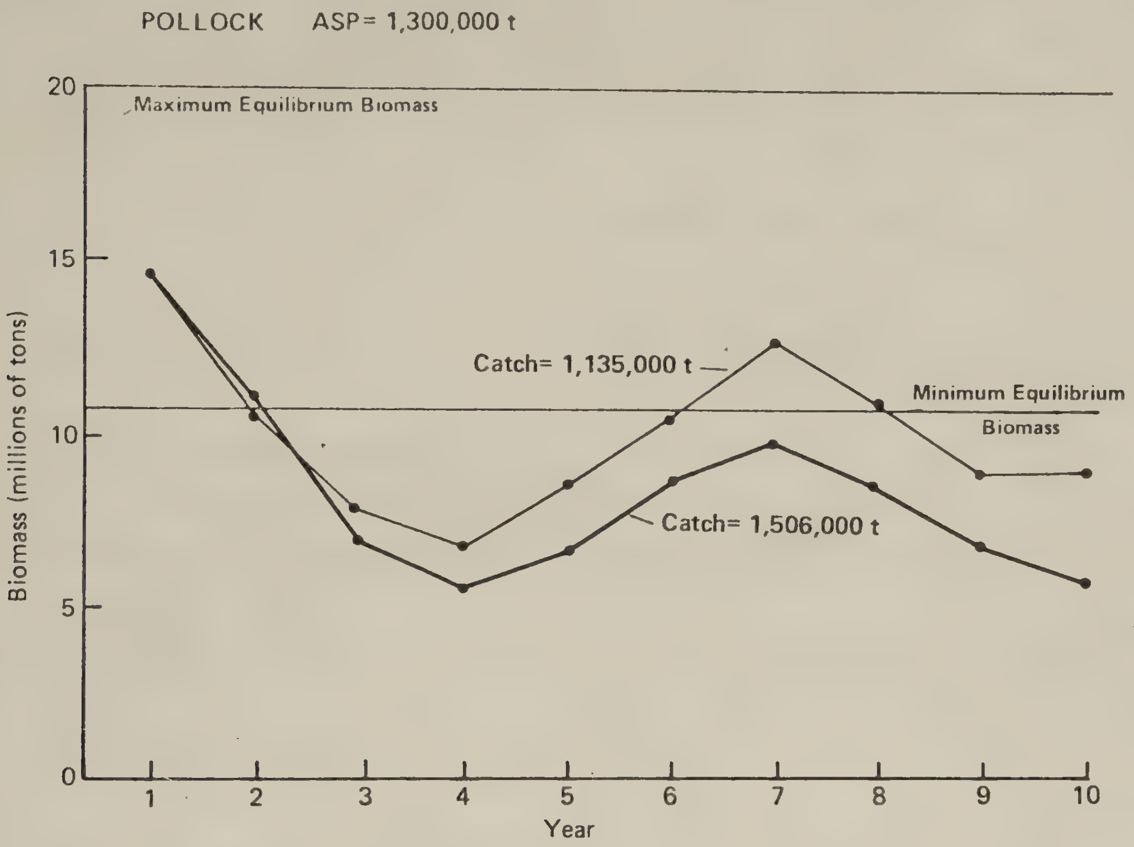


Figure 2. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for pollock.

Pollock (Figure 2): Abundance of pollock shows the widest level of fluctuation of all the groundfish species, largely due to its cannibalistic characteristics. The stock biomass is affected differently by simulated catch levels of 1.13 to 1.50 million t. At the higher catch level, the amplitude of variation is smaller and the population biomass is driven lower. The period of the cycle is 6 years, although Laevastu *et al*. (1982) have reported that temperature anomaly can shorten it to 5 years. Therefore, in a matter of 3 years, the stock biomass can drop from peak to trough by about 50% (Table 4).

Table 4.--Typical period and magnitude of fluctuations in biomass for the major groundfish groups in the Bering Sea under average conditions.

Species group	Period (years)	Fluctuation (percent)
Pollock	6	50
Pacific cod	5	8
Yellowfin sole	5-7	12
Turbots	7-9	20
Other flatfish	5	10
sablefish	6	20
Pacific ocean perch	No apparent cycle	
Other rockfish	No apparent cycle	
Atka mackerel	8-10	30
Total groundfish	5-6	22

The simulations show that the proper level of catch for the fishery should be set according to the current point on the biomass abundance cycle. Information from the single species analysis suggested that the biomass of pollock went through a period of biomass decline (1973-76), increased slightly from 1977-81 and may be on a down cycle near the peak. The 1983 ASP of 1.3 million t would, therefore, be on the high side, since biomass is expected to be driven even lower below the minimum equilibrium level for 3 years before the next up cycle. Therefore, it is suggested that the catch level for 1983 be set in the 1.1-1.2 million t range to help keep the population biomass at a higher level. This is a case example, where the model has suggested a catch level lower that derived by single species analyses.

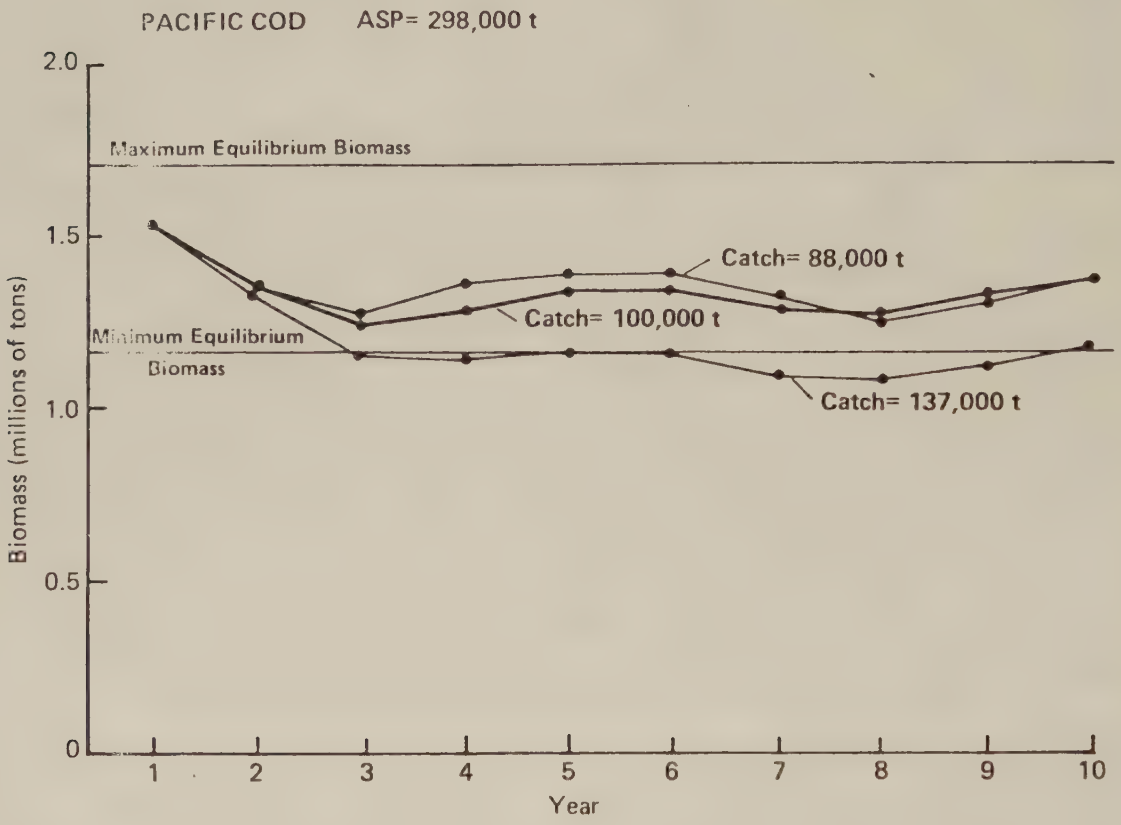


Figure 3. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for Pacific cod.

Pacific cod (Figure 3): In the case of cod, the long-term sustainable yield is about 100,000 t based on model simulations. Normal variations in cod biomass are not very large (± 8%) and has a weak periodicity of 5 years. However, based on single species analysis, it can be shown that variations can be much higher and that the current biomass of cod is at an unprecedented high level because of unusually strong year classes in the population. The ASP of 298,000 t is about 3 times larger than the long-term equilibrium yield. This ASP should provide a better basis for setting the 1983 catch level for the fishery because the strong year classes are expected to remain in the fishery for no more than another 3 years. It is, perhaps, more prudent to take advantage of the available surplus production now before it is lost to natural mortality.

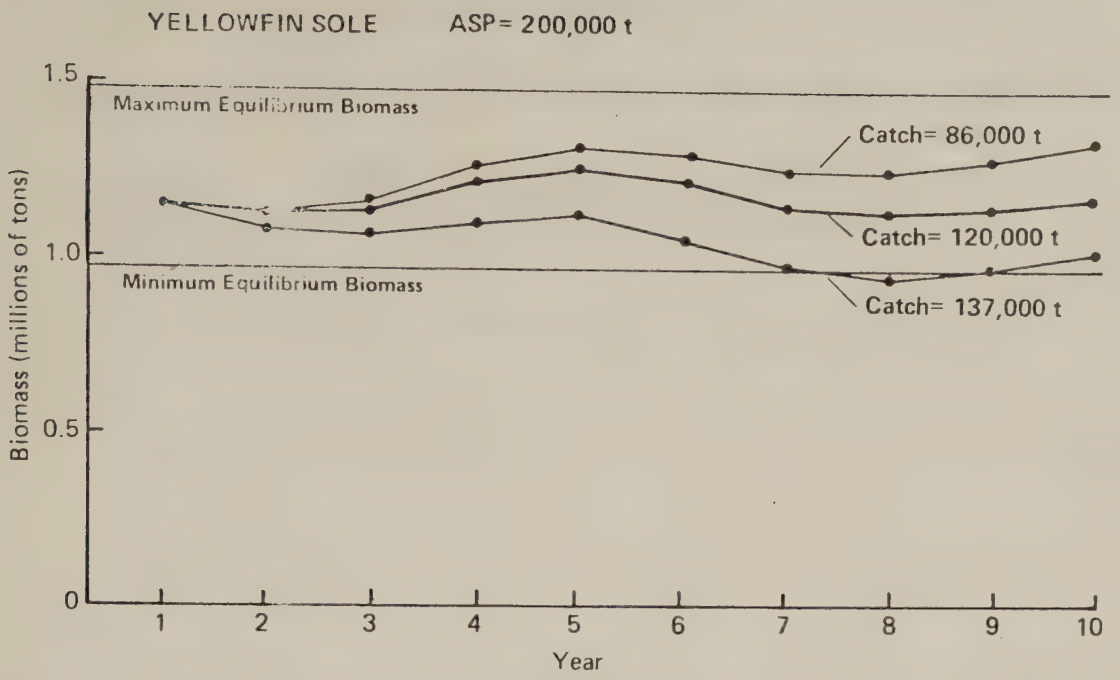


Figure 4. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for yellowfin sole.

Yellowfin sole (Figure 4): Model simulations show that the long-term equilibrium yield is about 130,000 t and natural fluctuations in biomass are not large (+ 12%). The period of the cycle is about 5-7 years. From single species assessments, on the other hand, it was noted that the yellowfin sole population is at an historic high and has been increasing rapidly in abundance since 1979 (Bakkala and Low 1982)1/. The high level of abundance is attributed to a succession of strong year classes. The 1983 ASP is at least 200,000 t. Since population abundance is substantially above the long-term maximum equilibrium level, it is prudent to harvest at the ASP level to take advantage of high surplus production. The 200,000 t catch level may also be beneficial to the overall ecosystem since it would contribute to drive the population biomass down towards equilibrium.

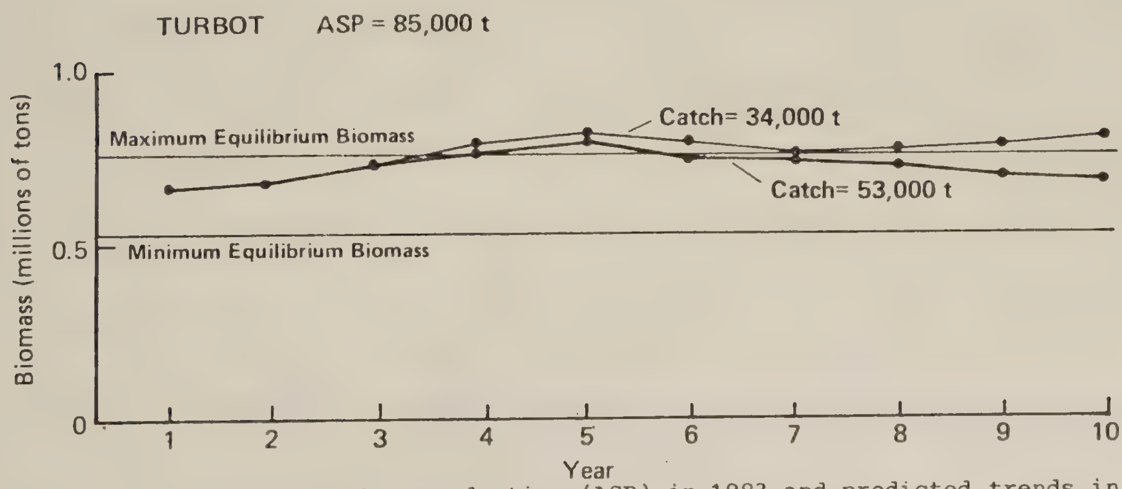


Figure 5. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for turbot.

Turbots (Figure 5): Turbots are made up mainly of two species, arrowtooth flounder and Greenland turbot. The species-by-species analyses show that ASP for the group in 1983 is about 85,000 t. The PROBUB simulations show that this catch level appears sustainable and will keep the population biomass within its equilibrium bounds. The simulations also indicate that long-term fluctuations in abundance are ± 20% over a period of 7-9 years.

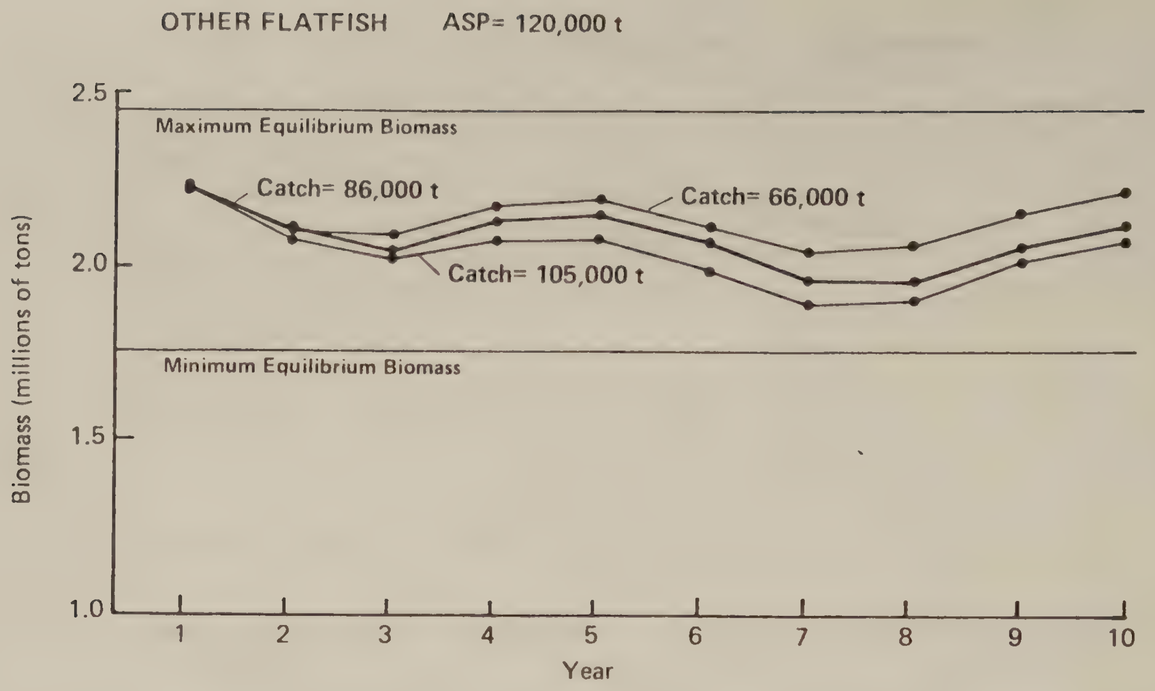


Figure 6. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for other flatfish.

Other flatfish (Figure 6): This group is made up of smaller size flatfishes. The major species are Alaska plaice, rock sole, and flathead sole. The 1983 ASP for the group has been estimated to be 120,000 t (Table 1). The PROBUB simulations show that this catch level appears appropriate and sustainable since it should keep the population biomass within its equilibrium bounds. The simulations also indicate that long-term fluctuations in abundance are ± 10% over a period of 5 years.

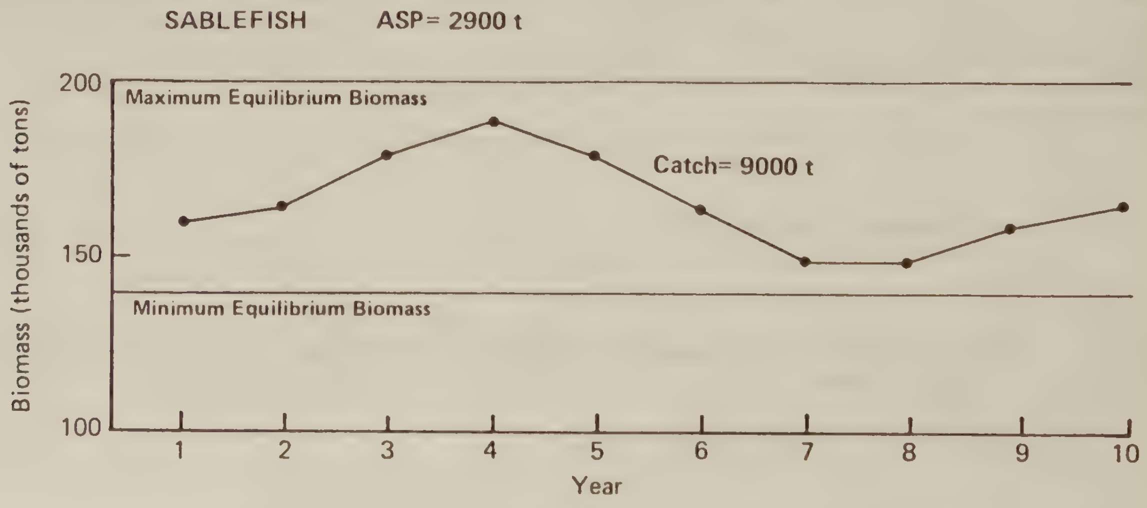


Figure 7. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for sablefish.

Sablefish (Figure 7): Single-species analysis shows that abundance of sablefish has declined from former levels of abundance in the 1960's to a relatively low and stable level in recent years. The ASP for 1983 has been estimated at 2,900 t. The PROBUB model, however, shows that the long-term abundance of sablefish is normally lower than the high levels encountered in the 1960's. It also shows that under mean equilibrium conditions, the long-term sustainable yield could be 9,000 t, or three times higher than the 1983 ASP. Since the present level of abundance may be close to the mean equilibrium condition, it is suspected that the 1983 ASP may have been too conservatively estimated and may be increased. The model also indicates fluctuations of ± 20% over a 6 year cycle.

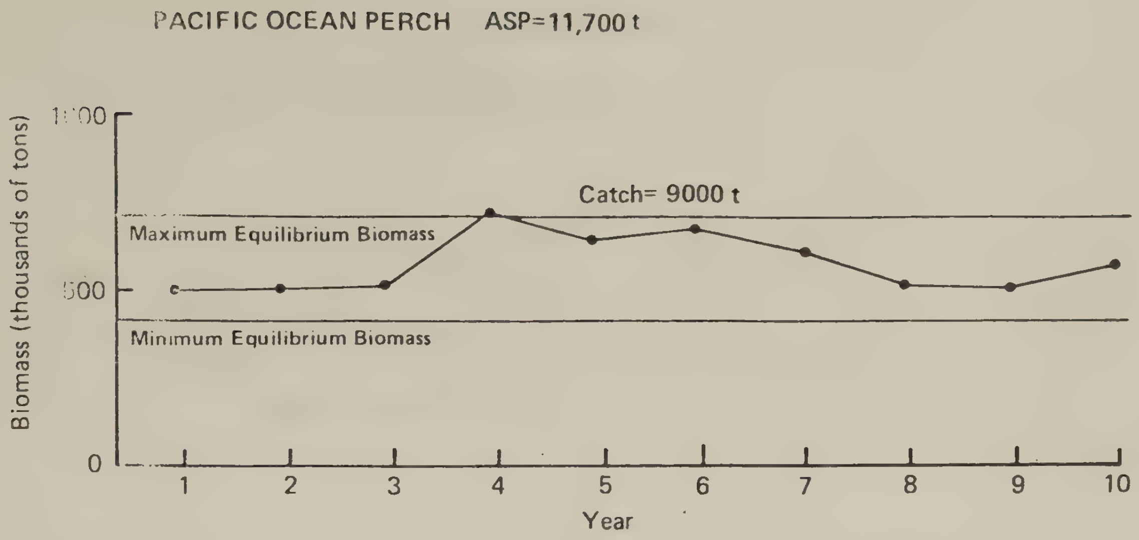


Figure 8. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for Pacific ocean perch.

Pacific Ocean perch (Figure 8): As in the case of sablefish, abundance of ocean perch has declined to a relatively low and stable level from former higher levels of abundance in the early and mid-1960's. The PROBUB model, however, shows that the present level of abundance is the normal long-term equilibrium trend. It also suggests that under long-term conditions, sustainable catches would be lower than the 11,700 t ASP estimated for ocean perch in 1983. Therefore, the catch quota for ocean perch should be set lower than 11,700 t and, perhaps, about 9,000 t as noted in the figure. The model does not show an apparent cycle of production.

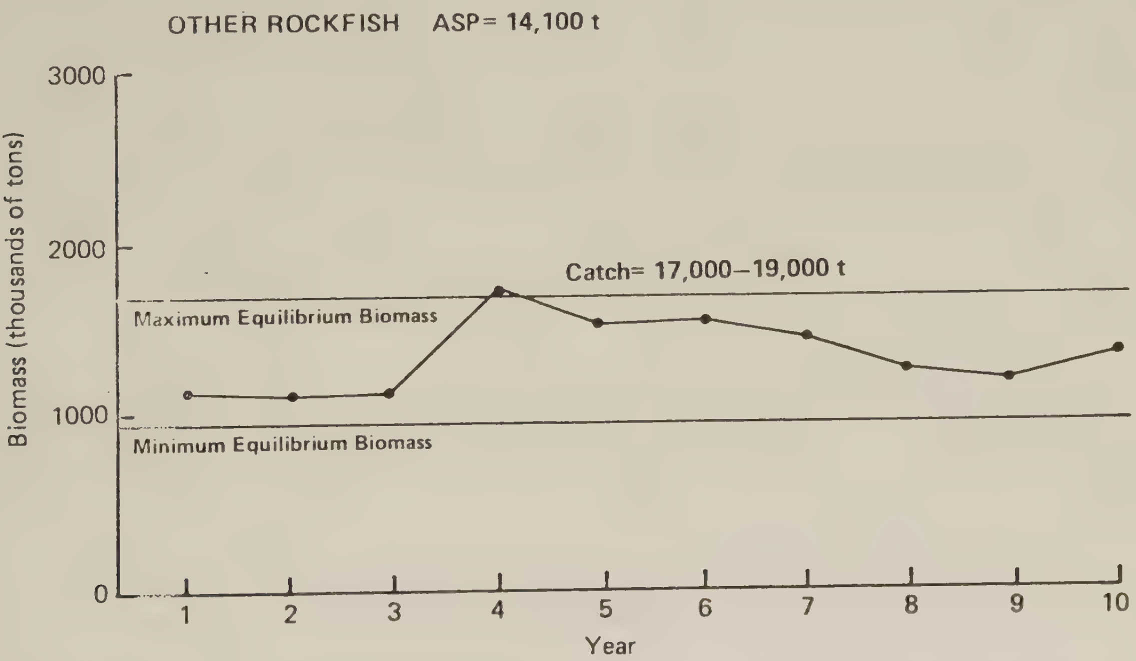


Figure 9. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for other rockfish.

Other rockfish (Figure 9): This group of rockfish is made up of more than 14 species of the *Sebastes* and *Sebastolobus* genera. The long-term abundance of this group is about twice that of Pacific ocean perch. The ASP for the group has been estimated to be 14,100 t (Table 1) which appears to be an appropriate catch level since the long-term equilibrium catch is likely not much higher. As in the case of ocean perch, the model does not show an apparent cycle of production.

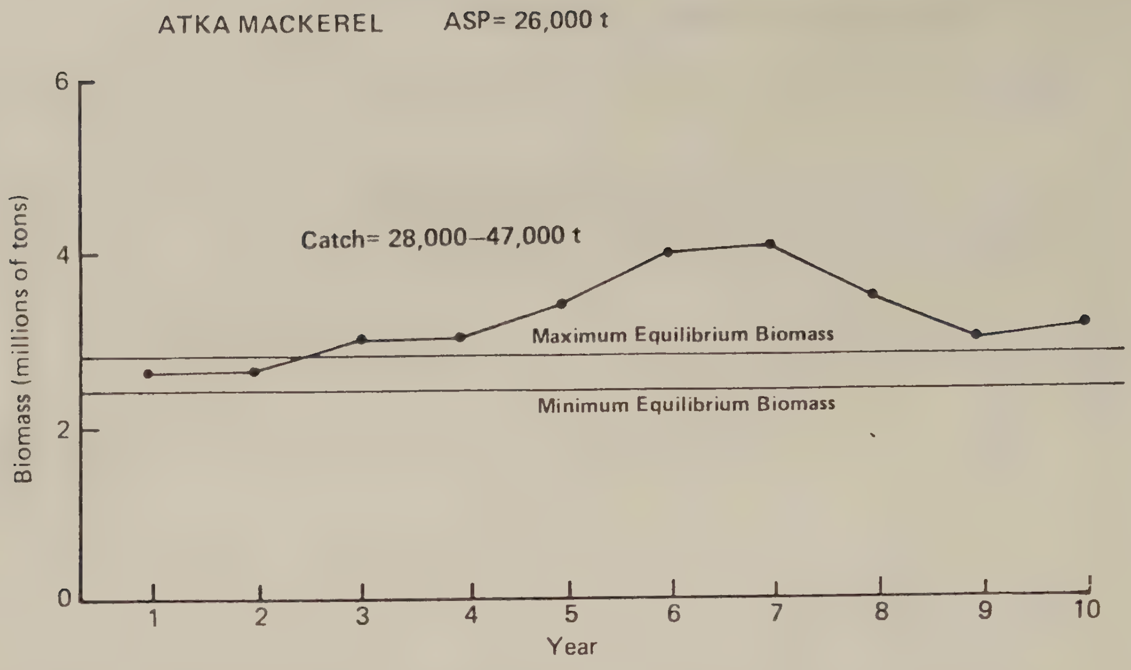


Figure 10. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for Atka mackerel.

Atka mackerel (Figure 10): The model sugests that Atka mackerel is the second-most abundant commercially important groundfish in the region. The resource makes up about 9-13% of the groundfish complex. Catch levels, however, are substantially lower than that of yellowfin sole because of its scattered semi-pelagic existence and lower commercial importance. Although the ASP level of 26,000 t was empirically estimated from catch trends and preliminary hydroacoustic estimations, the model shows that higher catches are sustainable. The simulations show that catches of 28,000-47,000 t have about the same effects on the overall biomass of the resource. Moreover, they also imply that catches in excess of 47,000 t may be sustainable since the population is above maximum equilibrium level. The simulations indicate biomass fluctuations of ± 30% over a period of 8-10 years.

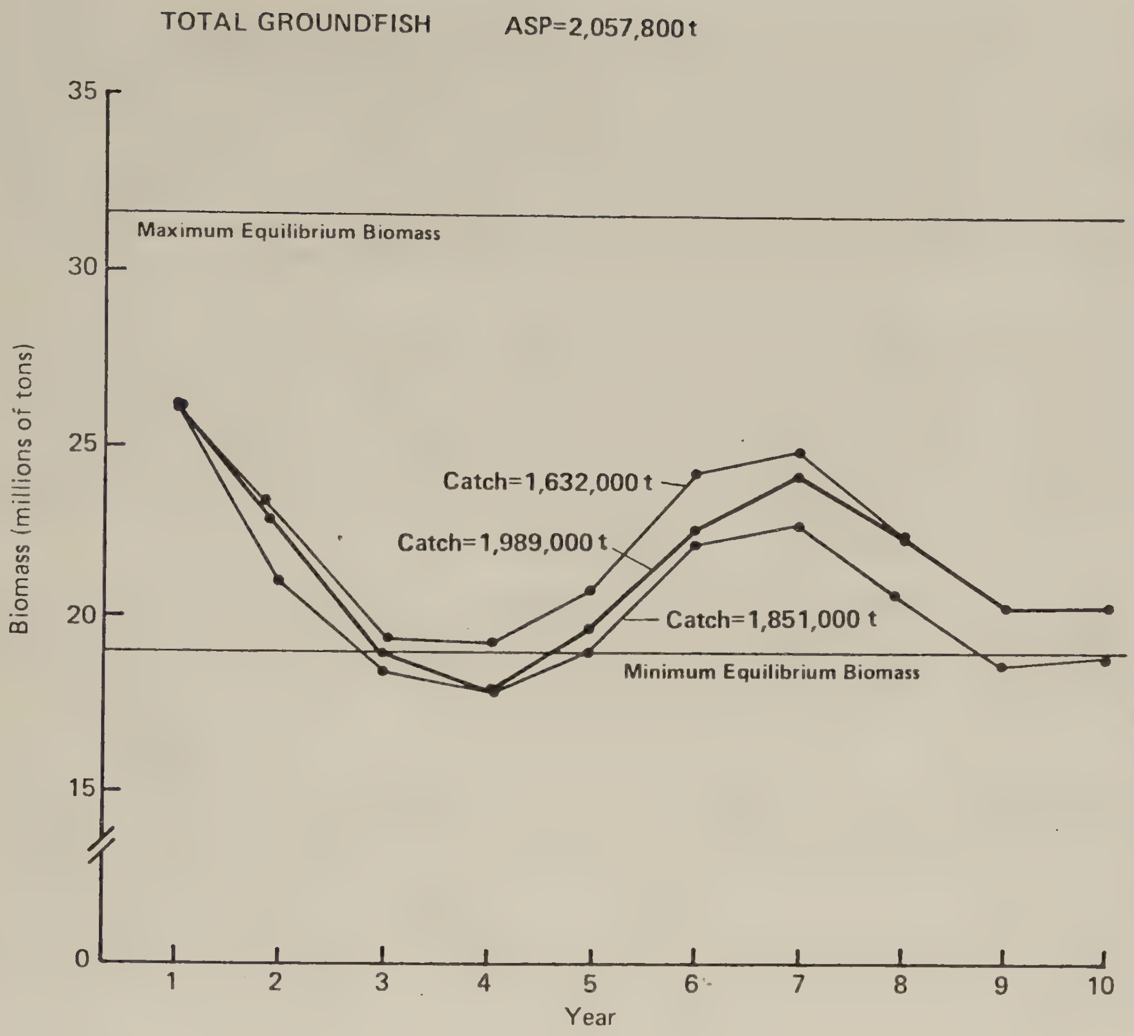


Figure 11. Annual surplus production (ASP) in 1983 and predicted trends in population biomass at selected catch levels for total groundfish.

Total groundfish (Figure 11): The PROBUB model shows that the overall biomass trend for the groundfish complex is strongly influenced by pollock. The total biomass would fluctuate by ± 22% over a distinct population cycle of 5-6 years. In general, an overall catch of 1.9-2.0 million t appears to be the long-term upper bound. A lower catch may allow the groundfish complex to achieve higher biomass levels and remain above the minimum equilibrium biomass level. The actual level of catch should take into account the relative position of the current level along the natural cycle of abundance. From single species analyses it is believed that abundance of the groundfish complex is very high and a catch of 2.0 million t or higher appears to be possible for 1983. However, the abundance of pollock is projected to be on the decline. Since pollock is the principal component species in the ecosystem, it is suggested that the total 1983 catch from the groundfish complex not exceed 1.9 million t.

DISCUSSION

The use of ecosystem models to complement traditional species-by-species analyses of data for development of management measures, particularly those on catch quotas, has taken on a more practical value for assessment and management of Bering Sea groundfish resources. This paper has illustrated that the PROBUB model may be used to evaluate long-term trends in biomass levels for the component species groups in the goundfish complex and can make a difference for setting regulations. The model, however, cannot yet replace the traditional species-by-species analyses for management since these analyses provide a great amount of essential details on current year-to-year changes to the trend, species composition, age structure, and other population dynamic characteristics of the stocks.

The use of the PROBUB model has resulted in considerations for setting catch quotas that are different from ASP's estimated for pollock, sablefish, Pacific ocean perch, and Atka mackerel. In the case of sablefish and ocean perch where abundances have stabilized at relatively low levels, it is an impulsive reaction to want to rebuild the stocks to former levels of abundance. However, the model has shown that the present low level of abundance may have been part of natural fluctuations about which little is known. Therefore, any desire for rebuilding the populations to former levels of higher abundance may not be realistic. It has reaffirmed that the estimated ASP's for turbots, other flatfishes, and other rockfishes are appropriate catch levels.

The model also shows that short-term fluctuations in abundance of yellowfin sole and Pacific cod could not be detected without additional model development, particularly to reflect environmental anomalies and their effects on populations. As such, the estimated ASP's via single-species analytical techniques which reflected the presence of strong year classes, are better criteria for setting catch quotas.

The PROBUB model is perhaps most informative for indicating fluctuations in production under average conditions. The biomass of pollock follows a distinct cycle of 6 years and can vary by ± 50% over this short period (Table 4). Since pollock is the most dominant species in the groundfish complex, the overall trend for the complex is the same as pollock. However, the magnitude and period of fluctuations are dampened a little by the other component species to ± 22% in a 5-6 year cycle. The model also shows that biomass of Atka mackerel can fluctuate by 30%, sablefish and turbots by 20%. yellowfin sole by 12%, other flatfish by 10%, and Pacific cod by 8%. A biomass cycle is not apparent for rockfishes, at least not over a 10-year period. Since rockfish are known to have substantially longer life spans, any cycle is expected to have a longer period.

Although the PROBUB model has been used to help set catch quotas, it may also be used to evaluate impacts of exploitation strategies that are not limited to catch quotas. For example, effects of proposed time-area closures to the fishery, changes in the species composition of the groundfish complex, and that of other trophic levels, such as those of marine mammals, can be evaluated through simulations. These simulations would be very useful for formulating management philosophies and policies.

REFERENCES

Bakkala, R., W. Hirschberger and K. King. 1979. The groundfish resources of the eastern Bering Sea and Aleutian Islands regions. Mar.Fish.Rev. 11:1-24.

Laevastu, T. and H.A. Larkins. 1981. Marine fisheries ecosystems: Its quantitative evaluation and management. Fishing News Books Ltd., Farnham.

Laevastu, T., R. Marasco and M.L. Hayes. 1982. Evaluation, harvesting, and management of fluctuating stocks. Oceans 9:761-765.

MODELLING FISHERIES: WHAT WAS THE QUESTION?

by

Gary D. Sharp, Jorge Csirke and Serge Garcia

Marine Resources Service
Fishery Resources and Environment Division
Fisheries Department
FAO, Via delle Terme di Caracalla
00100 Rome, Italy

Resumen

En este trabajo se revisa la evolución de los modelos matemáticos empleados en la evaluación y ordenación pesquera, tanto desde el punto de vista histórico como desde el punto de vista conceptual. Se subrayan los problemas que han surgido durante esta evolución tales como las variaciones en las capturas, la mortalidad, distribución, crecimiento, reclutamiento, escalas de tiempo y estructuras por edades. Se pone también énfasis en problemas de particular importancia, tales como el muestreo, el origen y la estructuración de hipótesis, así como los conceptos relacionados con los stocks, incluyendo la caracterización de los mísmos. Todo esto lleva a la pregunta en forma de conclusión de ¿por qué modelar las pesquerías? Se revisa la evolución y las diferentes alternativas que se han presentado y se presentan en el campo del modelaje en pesquerías. Se revisa el esquema conceptual, se compara el enfoque tradicional en los modelos de pesquerías y se dan algunas sugerencias en cómo pueden ser mejorados. Se hace una revisión de la perspectiva histórica y después se discuten algunos aspectos relacionados con los estados de no equilibrio de las poblaciones de peces, tales como las variaciones en las capturas, las variaciones en mortalidad, cambios en la distribución de las poblaciones, los cambios en crecimiento, la variabilidad del reclutamiento, las variaciones en las escalas de tiempo, variaciones en la estructura por edades, cambios en la captura por unidad de esfuerzo, la abundancia, etc. Se dan algunos ejemplos de cómo la selección de un determinado modelo tiene una influencia grande en los resultados y conclusiones que se pueden obtener de un determinado conjunto de datos. Se agrega un anexo donde se discuten los métodos empleados en la caracterización de poblaciones de peces.

INTRODUCTION

The mathematical models used in conventional fisheries science are abstract, simplified representations of the processes governing growth, decay and reproduction of exploited populations as well as their reaction to exploitation. As all models, they are only special cases of particular scientific theories. At any point in time they reflect, at best, some part of the knowledge and understanding we have been able to integrate in order to try and answer a specific question. Models must, therefore, change and new dimensions must be captured in the representation when our knowledge improves or when a different problem must be addressed. Many aspects of the models available to us for the last 3 decades are more and more often said to be unsatisfactory and it is probably time to check their appropriateness in face of the knowledge accumulated since their inceptions, but it is also time to ask whether the model is being applied to a situation which corresponds to the special case for which the model was developed.

A model can be a useful tool only when the problem addressed is well formulated for numerical analysis. It is therefore, useful to consider classical formulations of each fishery problem in order to compare the advanced point of view with the previous ones. It is important to recognize that the scientists who developed the original production or yield per recruit models based their work on the observation that the economically and biologically depressed resources of the North Atlantic recovered noticeably during the 1st and 2nd World War periods when fishing effort declined considerably.

The rapid development of fishing effort in the fifties rapidly raised questions about inherent limitations of resources particularly about the necessity to regulate fishing mortality. It was largely accepted that unregulated fisheries lead to economic, and possibly, biological overfishing. The problem to be solved was therefore, that of optimizing captures while conserving the resources by regulating fishing. Essential questions had to be answered such as: How do growth and mortality interact in the development of population biomass and production? What is the effect of additional mortality by fishing at different ages? How much can be extracted from a given stock? What is the relation, if any, between parental and progeny abundance etc.? Therefore, models had to be designed to investigate these since experimentation was and remains hardly feasible.

The same problems have still to be faced today but with new knowledge additional dimensions need to be added. The climate driven environment has been recognized as an important causal factor of variability of pelagic stocks, with or without intensive fishing, through changes in both recruitment success and geographic distribution. This has created the need for more reliable predictive "tactical" models usable in the short term for deciding on management measures in order to cope with continuous environmental changes. Of course ecological perturbations due to fishing are also likely since the removals are often selective and can be large proportions of major populations.

In this paper we try to retrace the evolution of modelling from the historical as well as from the conceptual point of view, underlining the problems that have been raised during that evolution such as variations in catches, mortalities, distribution, growth, recruitment, time scales and age structures. Emphasis is given to problems of particular importance like sampling, causality and hypothesis structuring as well as stock concepts including stock characterization which then lead us to ask again as a conclusion: "Why model fisheries".

FISHERIES MODELLING: EVOLUTION AND ALTERNATIVES

The Conceptual Modelling Framework

Our knowledge of species specific biology or understanding of ecological interactions has improved with time although most fisheries models basically rely on Russell's (1931) and Graham's (1935) original conceptions that the state of a single species population at any time was the result of growth, mortality, recruitment and migration processes. This has clearly been the basis for historical elaborations of all the presently available models including the most sophisticated ones. The different directions taken by fishery modelling stem from different perceptions about the key factors responsible for population changes, namely fishing effort, physical environment or predation.

The classical theory of fishery science has been based for a long time on a series of elementary models where natural mortality (M) is usually considered as an exponential process, constant after recruitment; growth (G) is represented by various continuous or discrete functions of size or age. Fishing mortality (F) is supposed to be proportional to fishing effort (f) and therefore catch per unit effort is equally taken as proportional to abundance. Biological production is mostly considered as a function of biomass and recruitment is often represented as a function of stock size.

Additional basic concepts or assumptions underlying the classical modelling of fisheries are those of steady state and homeostasis. It is believed that a given population is in permanent dynamic equilibrium with its environment and therefore, limited by some feature of it which defines a specific carrying capacity (K); that population abundance is significantly affected mainly by fishing; that a new steady state is reached when fishing is stabilized; and that the observed declines in productivity and economic conditions (attributed to excessive fishing) are almost certainly reversible (homeostasis).

The original conception of fishery systems models as closed,[1] steady state systems was quite in line with the conceptual framework of other branches of ecology and science in general at that time.

Modern science is however discovering that systems (and more typically biological systems) are more often likely to be open and affected by non-linear, non-equilibrium and often non-reversible processes, characterized by threshold limits and discontinuities. As the available data base builds up it becomes more and more evident that recruitment variations cannot be considered as random noise, but that this variation is an essential signal, input into the adult population system (the only portion of populations usually modelled). Recruitment is the 'output' of an adjacent system (the nursery) about which our understanding has been poor and therefore, usually neglected in general fishery modelling. It becomes clear that, at least for quite a number of stocks, a drastic revision of the 'original' models is necessary and, for instance, that the concept of "carrying capacity" of the environment applies probably more often at the larval stages of a population than at adult stages, and that recruitment may be affected by stock size but is certainly affected at least as strongly by environment.

The Classical Modelling Approach

Within the above conceptual framework the precursors in biological fishery modelling integrated the elementary submodels on growth, mortality, production, etc. in the two most widely used surplus production and analytical approaches of fishery science in order to predict fisheries performance. These approaches have therefore the defects of the elementary models and assumptions employed, aggravated by the effects of their combination.

---

[1] In the sense that the species and its predator (the fishermen) were isolated conceptually from other species interaction or from the environment

The limitations of these higher order models are well known and the literature is crowded with theoretical considerations about the possible effects of density dependence of growth and mortality, or about the effect of seasonal or long term variability of the subpopulation component interactions as well as trophic factors. However, because such effects are difficult to isolate and measure, they have generally not been taken into account in modern decision-making processes related to fishery management.

These models were constructed to investigate steady states of self-contained monospecific "unit" populations (as nearly closed systems) and their reactions to fishing. Density dependence was implicity accounted for in production modelling and could be introduced in analytical modelling as shown by Beverton and Holt (1957) themselves.

Despite their obvious limitations, the models traditionally used for management have had their indisputable usefulness. The Production Model was important in providing convincing arguments that resources are limited and that effort needs to be controlled if any conservation objective was to be reached on the long-term.

It can be said that production models should also have been strategic models (helping to identify possible objectives and ways of action). They have, however, been used with little success for year to year implementation of effort reduction policies or quota regulations and may be said to have often failed as tactical models.

Yield per recruit models gave clues about the puzzling problems of balance between growth and mortality and of the effects of 'thinning' of adult populations by fishing under different exploitation patterns. They have helped us to understand the effects of management measures as changes in mesh size and closed areas or seasons which, by the way, is what management has been about for decades. They finally showed, by ommission, that recruitment was crucial to understanding and prediction of year to year variations of stock sizes.

Towards Improved Modelling

Tersely stated, the problem is to either be simple or to be realistic. The situation described above is neither specific to fishery science nor to quantitative ecology in general. The fishery system is a very complex one. Modelling is necessary and, as always, compromise needs to be found between holism and practicality; between untractable sophistication and oversimplication. There will always be a need for partial analysis and modelling of the fishery systems, including in models the processes which are understood and documented, leaving out of the model (as externalities) the processes which are still beyond understanding and beyond control. The resulting simplification makes models more understandable but poses immediately the problem of interactions. As soon as it is recognized that the effect of externalities on the modelled sub-systems are far from negligible, it must be recognized that that specific approach is too narrow.

For example, in spite of the recent discovery and attention to relevant small time and space scales, proper modelling of recruitment will need to also involve observations of large time and space scales to take into account the phenomena of cross-oceanic or inter-oceanic teleconnections as well as low frequency signals like "sunspot cycles" and other related cosmic factors. However, it is quite evident that it is pointless to model recruitment without taking into account microscales (metres/days) in order to resolve particular time-space "survival windows" for the analysis of the mechanisms directly affecting larval survival.

In some cases a more comprehensive and realistic model would have to take into account species interactions as well, especially as far as food relationships are concerned, particularly when it is anticipated that predator-prey effects may be just as important, if not more so, than fishing effects.

Care must be however taken because there will also always be the tendency to develop as many holistic models as possible (energetic, trophic-dynamic, or self-generating models) trying to circumscribe in the model all the essential processes. The risk here is just as Hedgpeth (1977) states: "the construction of elaborate diagrams and mystic-mathematical representations of assumed relationships powered by selected values is a favourite pastime of many ecologists and environmental engineers and a model which is simply an elaborate mathematical summary of a textbook does not tell us more than we already know." Erwick et al. (1979) remind us that a model can be made so sophisticated as to produce outputs resembling closely the real world. However, because the underlying assumptions are so complex and their interdependence so obscure the model may not be easier to understand than the real process was (Bonini's paradox).

The very complex models such as the trophic-dynamic (Andersen and Ursin 1977) ones have a high number of dimensions and therefore, their data requirements are high. They use numerous coefficients and involve quite a lot of measurement and estimation. As proposed by Fedra (1980), they will certainly have a role in the development of fishery science but their usefulness for management can be questioned because their complexity and number of dimensions prohibit analysis of their sensitivity to variation and hence evaluation of their ability to reflect biological responses.

The goals of model building, namely realism, precision, and generality seem therefore just as conflicting as management objectives generally are. A trade off has to be made when modelling fisheries. The energetic (Paloheimo and Plowright, 1979) and trophic-dynamic models being still too far from any practical application to fishery management, they will have to be further developed as experimental exercises, in order to try to gain some understanding on the mechanism of biological production of complex multispecific systems and to identify the most likely key factors responsible for year-to-year variations, and the most useful data to be possibly collected economically in the future.

This will be a long process and in the meantime we have to adopt a practical approach. We still need models but they have to be simple, (lower predictive value but lower risk of error) and enable the right choice be made between management options, within some tolerable limits of uncertainty. The precision required must be adapted to the objectives of management and unnecessary (overvalued) predictive reliability or precision should be avoided, because of the underlying costs or mistakes. For instance, it may be important to understand the mechanism of recruitment survival but it is essential only to know which parameters govern year class strength and supply predictive capabilities (see Csirke 1980 for the Peruvian anchoveta recruitment or Garcia and LeReste 1981 for predictive models in penaeid shrimp).

It is quite clear that, in contrast with the past, a strategy has to be adopted for management, under varying environmental conditions, for many stocks, but the cost of doing so in the future should be lower than the present losses by not doing so and the overall efficiency of management should increase. One obvious consequence of dropping the steady state hypothesis is the great increase in the need for monitoring (of species distribution, species composition, recruitment survival factors, etc.) in order to increase the short-term forecast capabilities of models. It will always cost a lot more to predict accurately next year's catch than to detect the most likely trend or sign of variation for a more or less near future.

Another consequence is the need to introduce the concept of risk management. It must be clear that the models cannot be deterministic and that there is no single answer to a given problem. It must also be clear that introducing a random factor (stocastic elements) into a model is not very useful for short-term management as most of the environmentally induced fluctuations are autocorrelated. It has been recently proposed to use decision theory (Lord 1976, Laurec and Maucorps 1981). Applied decision theory depends very much on the weighting of the various outcomes, and these will vary greatly among various interest groups. The uncertainty of the environment, biological responses, market fluctuations, and other often neglected control mechanisms make the first steps into a modern "decision theory" based management system difficult to implement, but this is an obvious requirement for progress toward proper system management.

The Historical Perspective

A brief review of past fisheries investigations helps to give some insights into possible trends and alternatives for fisheries sciences in the future, particularly in relation to the problem of modelling exploited fish populations.

The origins of fisheries modelling can be traced to the beginning of the century, and the available literature provides important landmarks in the history of fisheries sciences that will help in understanding why we are where we are now, what alternatives have been used and which ones have still to be explored.

The first landmarks in the history of fisheries science are those of Hjort (1914) and Baranov (1918). Both were compilers of the "pre-World War" knowledge in fisheries sciences and inspirers of the succeeding generations of fisheries scientists; and not surprisingly most of their basic concepts are still fully valid today.

It is not our intention to review the work of Hjort and Baranov but it is worth mentioning the main characteristics of their work and their general approach to fisheries sciences. This can probably be well-described by just the titles of their respective two main papers: "Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research" and "The question of the biological basis of fisheries". They both looked into the biology of fishes as the major issue when trying to solve fishery questions. Fishing itself was considered as an important factor, but the hydrographical and biological conditions were considered to be at least as important as fishing, with respect to the fluctuation of fisheries and of fish stocks. Already in 1914 Hjort concluded that, in the case of the few species he investigated, recruitment was highly variable and that this was the major cause of the fluctuation of fish stocks. While pointing out that variability of the strength of year-classes was the main cause of fluctuation of fish stocks, Hjort also indicated that these fluctuations were driven primarily by the conditions prevailing at the time at which the development of the early life history stages of fish were taking place.

If we are to make an inventory of the alternatives presented by Hjort (1914) and Baranov (1918) we will certainly find that these were quite ample. All factors that we consider important now were probably mentioned and proper justifications for investigating most of them were given. Moreover, in light of what we know now, we can probably conclude that the relative importance assigned by Hjort to each of these factors was probably well balanced. Great importance was assigned to the investigation of environmental and biological factors and of the effects of fishing, but what is most significant is that great importance was also assigned to the investigation of the relationship between these three groups of factors.

This was more or less the situation in the so-called "pre-World War" era, but then came the two World Wars which changed the course of civilization and also the course of fishery sciences.

The First World War (1914-18) caused fishing activities to be suspended for four years in the North Sea, and when fishing resumed in 1919, there were the results of the first large-scale non-voluntary experiment which demonstrated that fishing was in fact a major cause of fluctuation of exploited fish populations. These results were particularly striking in the case of some highly valuable fisheries that before the war were heavily exploited, such as cod, haddock, halibut, turbot, etc. Catch rates were higher, fish caught were bigger and total landings augmented during the few years after the war, but all these started to regress to pre-war levels as fishing intensity increased.

These series of events are the source of inspiration for another generation of fishery scientists, amongst whom the most representative are E.S. Russell and M. Graham. From this generation those classical papers that can also be considered as landmarks in fisheries literature are the one on "Some theoretical considerations on the overfishing problems" by Russell (1931) and the ones on "Modern theory of exploiting a fishery" and "The sigmoid curve and the overfishing problem" by Graham (1935 and 1939).

These were the first real attempts to represent the dynamics of an exploited fish population through a mathematical model, and it is noticeable that their subject matter was the same, the overfishing problem, although their approaches were different. Russell set up the foundations of what we commonly define now as analytical models, while Graham started another school of analysis based on the global production model. The works of these two authors also reflect the general concept that has lasted for many decades with regard to the most likely cause of fluctuation of exploited fish populations to be analysed and incorporated into fisheries models: the effects of fishing.

The Second World War (1939-45) gave a further large scale demonstration of the severe effects of fishing on exploited fish populations, and particularly demonstrated that the effects of fishing were reversible. This gave new impetus to the development of theories and models of population dynamics as well as new concepts of alternatives for exploited fish populations. The major factor remained fixed, i.e., the fishery.

The potential role of environmental and biological variability as major causes of fluctuations in fish populations was never completely ignored, but was conveniently relegated to just a potential role. In fact there were very few experimental observations to counterbalance the well accepted evidence that fisheries accounted for substantial amounts of the observed fishery and fish stock variabilities.

The works by Beverton and Holt (1957), Ricker (1958) and Schaefer (1954) are probably the best examples of the bloom in the development of post-war fisheries modelling. The models proposed were based on the assumption that fishing or fishery related factors (fishing mortality, average size of individuals, spawner stock size, size at first capture, etc.) accounted for most, if not all, of the variability of fish populations. A well founded concept if we take into account the events that affected fish stocks and fisheries in Northern Europe in the first half of the century. If the Northern European fisheries had been hit by a series of "El Niño" type of short-term climatic events instead, it is certain that the evolution of fisheries science would have been completely different, but that would have been true for world history as well.

The developments introduced by Beverton and Holt (1957) and Ricker (1958) to analytical modelling of exploited fish populations, and the ones introduced by Schaefer (1954) to global production modelling contributed to building an entire theory about how fish populations behave and on how to manage fisheries. There have been some later refinements and descriptions of special applications of these two schools of analysing and modelling fisheries for the purposes of fisheries management, but in general terms these developments can be considered as the ultimate steps in modelling the effects of fishing on fish populations. These two types of models do provide a reasonable framework for the development of fisheries management strategies as they stand now, provided that (a) the effects of fishing on the population can be measured and controlled, and (b) it still holds that most of the variability of the population characteristics is due to fishing. Beyond what has been achieved so far probably little more can be added to fisheries modelling by further efforts to improve modelling the effects of fishing, unless the effects of hydrographical and biological factors are brought into the picture with considerable effort to inter-relate each to the others.

It is certainly not fair to say that the development of fisheries science and of fisheries modelling have been slow, but it is true that although it had developed in both theoretical and practical aspects, most of this development has been concentrated on only one of the three possible sets of alternatives that were identified almost 70 years ago. The investigation and modelling of fishing effects on fish populations have developed, but the investigation and subsequent modelling of environmental effects and biological reactions and interactions has been disregarded for a long time.

Major attention has been paid to factors other than fishing in relation to the fluctuation of fish stocks only after the collapse of several important pelagic fisheries. The collapse of the California sardine in the 1950's; the collapse of Japanese sardine in the 1940's and sudden recovery in the 1970's; the collapse of the North Atlantic herring in the late 1960's; the collapse of the Peruvian anchovy in the early 1970's and the associated increase of other pelagic stocks, all contributed to more attention being paid to "the other" possible causes of changes in the fish stocks, although in most cases the first act was still to blame the fishery for the collapse of the fisheries.

Although it is true that no fishery will collapse in the absence of fishing, in most cases it seems that other (i.e. environmental) factors had either favoured the over-development of fisheries prior to the collapse or had complemented the negative effects of heavy fishing by reducing the growth potential of the subject populations.

Changes in recruitment are the major cause of fluctuations in fishable populations. Although normally more attention tends to be paid to downward than to upward changes, in fact, attention should be paid to both. The successive failure of recruitment has been identified as the most immediate cause of reduced stock size and subsequent collapse of the fisheries, but in most cases these have been preceded by a series of increased recruitments, that increased both stock abundance and subsequent fishing activities, thus magnifying the downward changes in the fishery resources when or if more usual recruitment levels resume.

Although the potential effects of change in growth rate and natural mortality (e.g. the post-recruit stages) are not as great as those caused by changes in recruitment, these can still play an important role in fish stock variability and attempts should be made to model their fluctuations for incorporation into fishery models.

Probably the most striking example of recruitment failures and subsequent collapse of the fisheries is that of the Peruvian anchovy in the early 1970's. The collapse occurred in 1972, but the conditions for it started building up at least two years earlier. The Peruvian anchovy also provides a good example of the potential effect of changes in growth rate. In fact a good recruitment entered the fishable stock in 1976, raising the total biomass to 11 million tons at the beginning of the year. However, reduced growth rate (and heavy fishing) contributed to reductions in stock size by the end of the year to around 3 million tons, thus extinguishing the expected recovery of the stock. It is worth noting that both series of events were linked to changes in the environment that respectively affected either reproduction success or adult feeding success, hence lowered growth in numbers and biomass.

Efforts need to be made to model changes in recruitment, growth rates, natural mortality, etc. and to relate these with environmental factors, but for this to be successful further investigations are needed on the relationships between these factors and, of course, on the factors themselves, how they work, how to measure them, particularly since most data available to date was collected to answer the question of how fishing affects fisheries.

SOME ASPECTS OF NON STEADY STATES IN FISH POPULATIONS

When trying to internalize in the models more externalities than in the past, essential phenomenons have to be considered, like patterns of variations in catches, mortalities, distribution, growth, recruitment and time scales.

Catch Variations

Caddy (1983) has provided an assortment of examples of four classes of fishery resource behaviours: I) Steady state fisheries; II) those with regular periodic fluctuations; III) fluctuations with irregular periodicity; and IV) irregular or intermittent production. Many examples of each type are available. Classical production models and age structured models may suffice to portray types I and II adequately for most management purposes. However, types III and IV will certainly require far more extensive information pertaining to causal, environmental and ecosystem related effectors.

Mortality Variations

All mortality is "event" controlled; a series of hurdles or irregular filters imposed at each stage, differing drastically from point to point in space. Much as fish school sizes are often distributed in a negative binomial fashion, predators are also often "aggregated" this way. There are also density related thresholds of abundances of egg-larval fishes and their prey which are important for feeding, hence survival. The predator relying on egg-larva sized prey, or larvae feeding itself, requires encounter threshold densities in order to affect survival/mortality of their prey.

Much of the earlier modelling effort has been based on "average" information or probability estimates based upon over-integrated data sets rather than relevant scales of interaction such as those employed in the studies of Vlymen (1977) and Beyer and Laurence (1981). The hurdle concept evolved by Beyer (1976, 1980) has a very strong probabilistic component, but is at least intuitively satisfying in this regard as presented. This type of modelling needs to be merged with data on the distributional properties of predator fields, their sources, etc. But, quickly one arrives at the point that it is the universe needing described and modelled. What should be done? What is sufficient information, where should one start and when should one stop?

The search for precision has always had its advocates, and it should never be given up. However, in fishery related field research the available tools are simply too coarse to yield other than rough indices at present. The most productive use of day to day research resources would be on gathering basic information about where, when and what is caught by various gears; where and when reproduction appears, where and when young stages are observed, particularly if it is possible to have precise ages of these. Time series of climatic conditions on a daily basis would be useful over the region their fisheries occur. Ageing via daily growth rings in pelagic fishes; larval blooms and juvenile migrations in estuarine fisheries; and general age-specific geographic distribution time series probably tell more about the present status of a fishery than most other information.

For example, the hypothetical annual and interannual variability in eggs produced and subsequent recruits realized shown in Figure 1 gives far more information than, for instance, simple egg-recruits tables. Seasonal changes in survival rate of progeny are not unusual in many species. However, it would be even more useful to have the time series data on both the egg-larval distributions (a lā Santander et al., Watanabe, this volume), and adults (ā la Kondo, 1980) in order to better understand their trends and possible interactions (Csirke 1980, MacCall 1981).

Once a time series of data of these sorts is available it is quite obvious why the simplistic "stock-recruitment" relationships can be both incomplete and uninformative. Even in some cases poor knowledge of the whole system can lead to erroneous interpretation, for example, Figure 2 drawn from Garcia (1983) for depicting seasonal changes in recruitment survival in shrimps has been modified in order to show the kind of year-to-year changes which are often "projected" into artefactual stock recruitment curves, without regard to system variables.

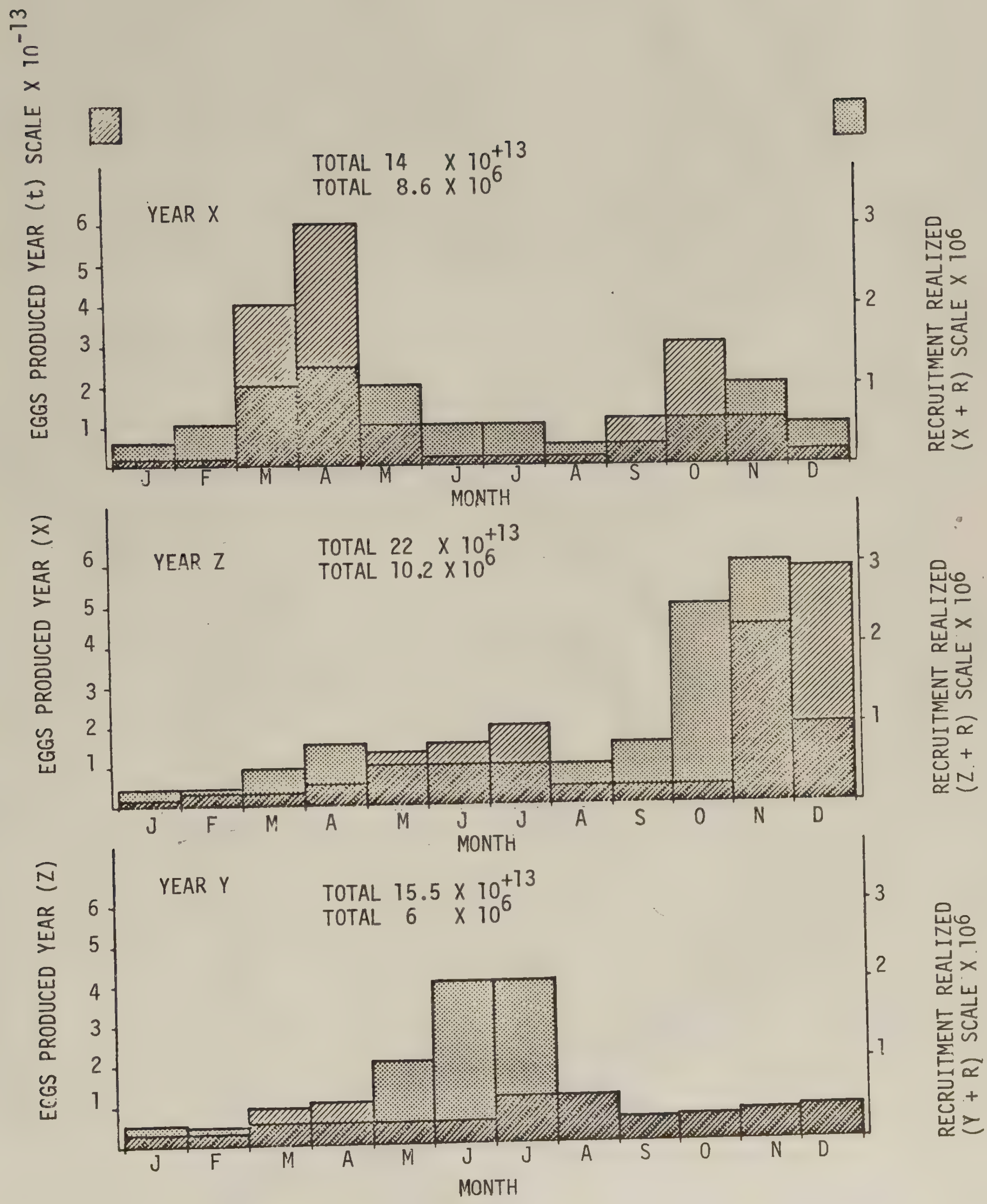


Fig. 1. Three hypothetical examples of monthly egg production and subsequent realized recruitments are shown. Note that although either total eggs produced or total recruitment may not be very different there is no suggested relation between either, or when survival, hence recruitment is determined.

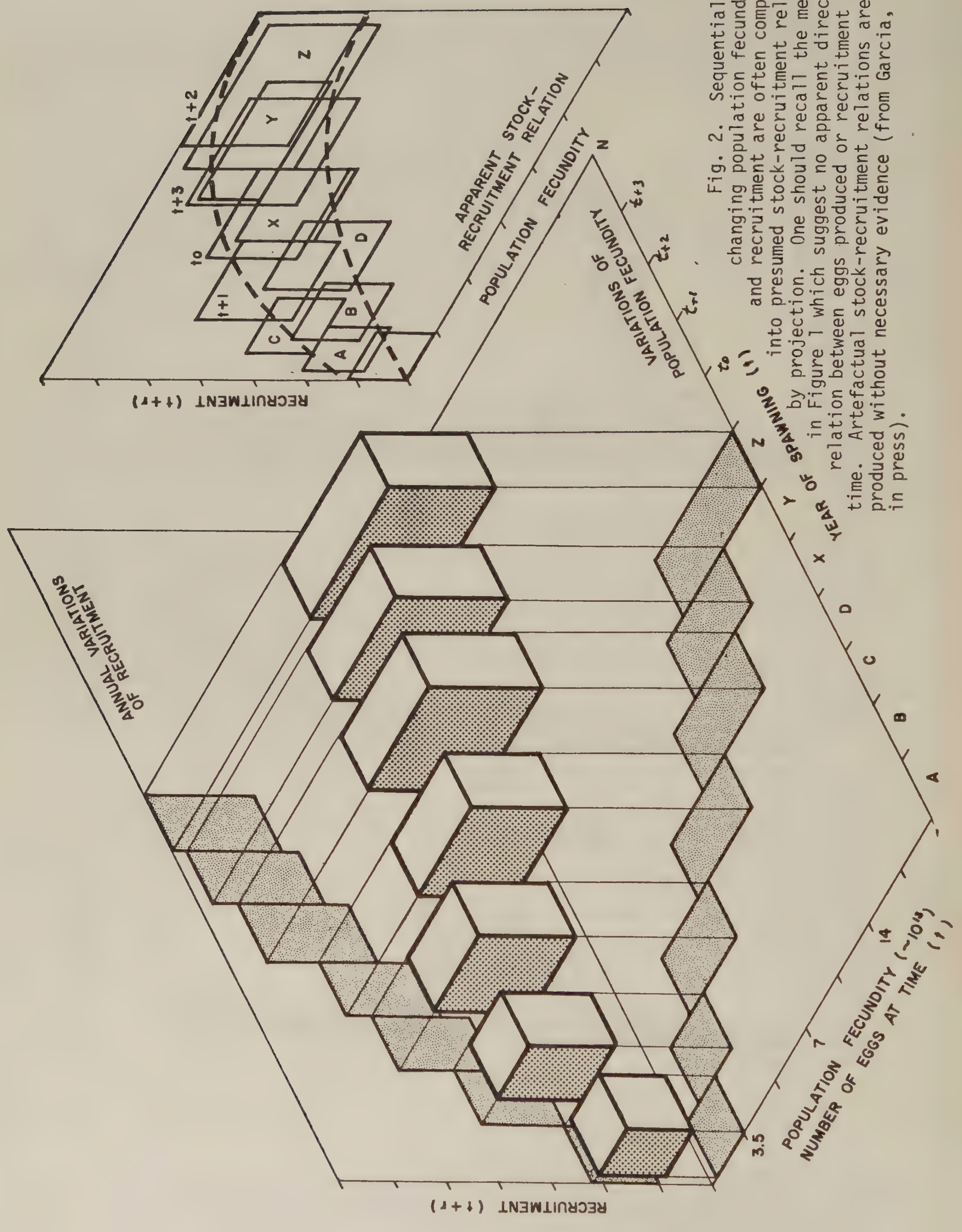


Fig. 2. Sequential changing population fecundity and recruitment are often compressed into presumed stock-recruitment relations by projection. One should recall the message in Figure 1 which suggest no apparent direct relation between eggs produced or recruitment in time. Artefactual stock-recruitment relations are often produced without necessary evidence (from Garcia, in press).

Modelling of non-equilibrium populations is slowly coming of age. Age structured models are commonly employed in which size-age data are arrayed in time-series such that from total catch and estimates of M and F, recruitment can be estimated. Assumptions are made about the relation between fishing intensity (f) and relative fishing mortality (F) i.e., fq = F, and either f or q (the so-called catchability coefficient) are held relatively constant. These models are appropriate for small regional fisheries with relatively direct concurrence between the population being exploited and fishing effort distribution. However, if there is emigration or migration such that the effort distribution is not concurrent with the resource, then knowledge of the In and Out proportions need to be known. If these estimates or assumptions are invalid then the model results are simply artefactual.

Species with diverse discontinuous fishing effort applied to them are certainly not easily modelled and this is a problem where population structure is vague and unknown. Age structure changes need to be evaluated from knowledge of both the distribution in time and space of the fishery and the age groups of the fish.

Distribution changes

Csirke (1980) was able to model the dynamics of recruitment in the Peruvian anchoveta utilizing catch and effort data as a measure of density and the relation between this and independent population size estimates as a measure of area, hence volume of the occupied habitat. The density dependent mechanism (density per unit volume) for recruitment modification can be attributed to density related cannibalism of the eggs and larvae by adult anchoveta (Santander *et al*, this volume).

Growth Changes

In many studies (e.g. Jones and Hislop, 1978; Zijlstra, Dapper and Witte 1982) there are clear examples showing modification of growth at various ages/stages, from early juvenile (prerecruit) to adults. In adult stages these changes in growth are related to changes in individual fecundity and often age of first spawning, all of which need careful analysis in order to understand the resulting reproduction success and subsequent recruitment. (Fontana 1981).

In the younger stages, the variables affecting growth reflect both biological distribution variations and also physical-chemical ones. Temperature, food particle distributions and predation appear to dominate larval growth and survival parameters (Theilacker and Dorsey 1981, and others - see IOC Workshop No. 28).

Changes in growth with time, associated with changes in either the overall abundance or the environmental conditions are also important and need to be given careful consideration when modelling non steady state fisheries. For instance, Zuta, Tsukayama and Villanueva (this volume) show that in the Peruvian anchoveta there were drastic losses in weight (of up to 36% for a given length) associated with abnormal environmental conditions and due to the high concentrations of the population that occurred in 1976-1977 and 1982-1983 even though there were no indications of changes in growth in length (Pauly and Tsukayama, this volume). Changes in growth with time and space are also shown for the Pacific mackerel and anchovy of California (Parrish and Mallicoate, this volume).

The Variable Recruitment Issue

As most population variation is explained by changes in natural mortality (M) at some stage in the life history, it should be asked where this might be accounted for. Of course, the usual mechanism involved is "a change in recruitment" which involves changes in either M or fecundity-related potential recruitment. Actually it is due to convenience of data availability that fishery models have to-date depended primarily on the post-age-at-entry portions of populations, and that these groups are assigned constant M values. This latter assumption is among the more troublesome in interpreting, for example, cohort analyses or other age structured models, and is simply blurred in the production models to such a degree that any changes in size-age structure for whatever reason and subsequent changes in "intrinsic rate of increase" (i.e. growth rate and mortality) are confounded.

There are several logical issues which should be examined in this set of "conventional explanations" before applying these models. These derive from a cursory understanding of fish life histories and an emerging literature on what comprises natural mortality at various stages. The fate of most dead fish is to be consumed by other organisms. The capture and engulfing of a fish is direct predation (M_{p1}). This is enhanced by the prey being debilitated through disease, poor nutritional condition, or senescense. However, good predators also consume healthy, viable prey, but may have to work harder to obtain their meals. There are secondary forms of predation (M_{p2}) such as scavenging, fungal or bacterial actions. Of course, this brings up the size hierarchy of direct predation, which often breaks down in secondary predation. That big fishes eat little fishes is no surprise, but it does appear that it is often forgotten that big fishes start out as little fishes, i.e. that the proportion of little fishes during their progression toward larger sizes is controlled by the amount of predation and therefore the abundance of predators in the system at various sizes.

Without fisheries operating, natural populations comprise a larger proportion of larger, older fish. The relative stability of such systems depends nearly entirely on the predation/consumption rates on smaller individuals somehow balancing losses at the larger sizes, i.e., lost due to senescense, disease or the limited predation by very large predators. The bulk of fecundity is usually bound up in large-old individuals in such systems. Once a fishery begins the older, larger individuals are preferentially harvested, and a flood of "uneaten" small fish is left to grow into older, larger individuals. However, under exploitation of the larger predators, not only do we expect a surge of survival in the intermediate sizes, but we also expect an increased predation upon the smaller individuals due to this removal of the larger, more ecologically efficient classes, i.e., fish generally have lower per-unit-weight nutritional demands as they grow. Remembering that these are system processes, rather than single population characteristics, we should find that the prey species preferred by the juveniles or pre-recruits (intermediate sized fishes) of each exploited population should be subject to increased mortalities, while these intermediate sized fishes' natural mortality should actually decrease in the exploited system from which their predators are being removed.

In any situation where cannibalism plays a major role, i.e. filter feeders and many opportunists like tunas, gadoids, etc., the fishery related changing predation rates represent variable M at age-size. In complex ecosystems comprising vast species arrays and diverse behaviours it is not so easy to pin-point which fishery is affecting, secondarily, which age-size-species, but the obvious point is that M values are neither stable, nor only a "species specific" character, they will depend to a great extent upon the ecosystem and its exploitation modes.

By definition the recruitment (R) criteria are fishery and gear specific, but the fluctuations in R will also reflect system variation of the sort just described. Any population can be said to have a finite recruitment potential in the numbers of viable, fertilized eggs it introduces into the sea. Of this potential, only some very tiny fraction will reach maturity, and contribute to the potential of subsequent generations.

Time scale variations

The difficulties with estimating natural mortalities are immense. The recent approach by Csirke and Caddy (1983) to equilibrium systems would permit estimation of M if a low variance, steady state system could be identified. However, the probability of any fishery resource being in relative steady-state changes with the number of species it might interact with and their (the predator's) mobilities; the reciprocal of its distribution area compared to its potential habitat; as well as the reciprocal of the number of age classes within the population. This latter problem is particularly relevant in that for descriptive expressions employing differential equations $(\frac{dx}{dt})$ where t is time, the time frame needs careful consideration. Differential equations refer specifically to time intervals where dt is small, i.e.$\simeq 0$, whereas t is often expressed as months or year long periods in fishery formulations. The assumption of year-wide responses, to say decreased adult abundance in recruitment process applications, is that for each species, and population component, the expected response time t is a reproductive life-span. For example, a fish living up to 13 years with maturity at age 6 has eight years to "reproduce itself" whereas our fishery models often expect any responses to perturbation to occur "instantaneously", i.e. in one year. Simulation modelling has shown us that when employing simplistic density dependent self generating models there is a resonance period of several reproduction cycles before "steady-state" is approached. This implies that perhaps only short lived species can "live up to" the assumptions of such models, and long lived fish cannot be adequately portrayed using models with only annual or shorter response time increments. It does seem rather foolhardy to expect that a population whose age structure is being collapsed due to fishing pressure will respond in the same fashion as the unfished or lightly fished one might. The "survival insurance" of many age classes is being harvested also, from which it is obvious that any selection over time for a minimum longevity guaranteeing persistence beyond long term perturbation processes can be reversed, i.e. early maturation and shorter, slower growth may be selected for by removing individuals of above average sizes from the virgin populations. Certainly changes in growth rate and age structure need to be accounted for, while the significance of the time increment should be considered in regard to the intensity of fisheries operating on the population or in regard to the intensity and variations of seasonal and epochal anomalies affecting local hydrography, and the behavioural characteristics of the population, i.e., its distribution, aggregation and migration characteristics, among many other ecological details.

All of these variables can and do affect natural mortality in a population, leading to variations or oscillations throughout the ecosystem.

Ursin (1982) has provided an exceptionally insightful discussion of the relative stability of marine ecosystems, based primarily on North Sea studies. His studies of predation (starting with Andersen and Ursin, 1977) lead him to look for stabilizing mechanisms such as the "triangular meshes" of a food web which he describes in some detail. Ursin's Table 2 (p.65) gives an interesting summary of Pauly's (1979) study of Gulf of Thailand trawl survey results, which can be contrasted with other systems.

Table 1: Changes in stock sizes of commercial species in the Gulf of Thailand, (Ursin 1982 - from Pauly 1979). Two significant digits retained.

Ecological group	Units of 1000 metric tonnes		
	Virgin stock	Exploited stock	$\frac{\text{Exploited}}{\text{Virgin}}$
1. Large benthos feeders	150	1.3	0.0087
2. Small demersal prey	830	21	0.025
3. Intermediate predators	620	74	0.12
4. Large predators	21	5.3	0.25
5. Pelagic fishes	13	5.7	0.44
6. Flatfish	3.5	7.6	2.2
7. Squid and crustaceans	30	90	3.0
Deplenished stocks (1-5)	1600	110	0.066
Replacing stocks (6-7)	33	97	2.9

Ursin concludes: "Obvious collapses of exploited stocks are few and limited to heavily schooling pelagic stocks, mostly or exclusively clupeoids. Most other fishes of temperate seas and of subtropical upwelling systems appear to be to a large extent ubiquitists and 'opportunists'. Contrary to this, the demersal fisheries of the tropical Pacific interfere with an extremely old and highly specialized ecosystem... In these, large longlived demersal feeders as well as shortlived pelagic feeders maintain large stock sizes in spite of heavy fishing.... In the demersal fisheries of the Gulf of Thailand... both of these groups collapsed quickly under fishing pressure whereas large pelagic predators were reduced only to half their former stock sizes."

From Table 1, it is obvious that populations of flatfishes, squids and crustaceans grew in the face of the decreases in the other groups. One should wonder what the usual pattern of variation might be in the Gulf of Thailand, with or without fisheries. Assuming stability is certainly questionable, but it would be nice to know just how much fishery operations perturb or contribute to natural fluctuations.

Age structure changes

Since we know already that an unexploited (by man) system will tend to comprise many older, high fecundity individuals with low-specific consumption requirements, it would appear that each species would tend to respond through long term selection to system perturbations such as changes in primary production rates, changing temperatures or even predation due to sporadically appearing nomadic predators, by promoting larger-older individual's abundance, increasing age classes, and generally shortening smaller, immobile stages as much as possible, i.e. maximizing growth rate and efficiency. Fisheries operate in opposition to this set of characteristics.

Whereas many pelagic fish species have managed to accomplish only the latter few things, many cannot reach large size and thereby decrease their predator field. Clupeids, engraulids and numerous bathypelagic species are in this group. However, some other species have evolved not only rapid growth, older-larger age classes, but also formidable sizes, i.e. the large sharks, the genera *Seriola*, *Scomberomorus*, *Thunnus*, *Coryphaena*, the istiophoridae and *Xiphius gladius*. These species are usually apex predators of omnivorous habit, high activity and mobility, and can be extremely ecologically inefficient (Sharp, 1983) in contrast with demersal or sedentary predators.

The opposite extreme is the situation for substrate specific populations, i.e., tropical reef fishes or tidal zone inhabitants where the populations are smaller in absolute numbers, life times are fairly short and even the size of potential predators is limited by the environment, i.e. refugia. Here the physiological and morphological adaptations for surviving the rigours of the environment are prerequisites. Variable growth or limited size, territorial behaviour, brooding or rearing of younger stages in those species with low fecundity, etc. are all demanded by "the Environment" if a species is to thrive. Yet the absolute adult population sizes are set by the number of appropriate home "sites", or substrate occupied, because any other than those individuals "on site" and actively maintaining their tenancy will be washed away, preyed upon or otherwise kept from occupying permanently "a site". What is interesting in this case is that exploitation of such species will open sites and tend to decrease natural mortality in the population at large, up to the point where fishing mortality is greater than the limiting "site" recruitment rate which will depend both on females "on site" as well as their abilities to produce sufficient young to fill any available sites. A reef fish assemblage may actually vary primarily in response to the very sporadic reductions of individuals in localized contexts which can also be subsequently recolonized by other, locally abundant species. This would make modelling reef fish communities very much more "fragile" than modelling either pelagic or demersal communities, due to the fact that as available substrate varies, reproduction rate varies as a function of "on site" individuals; natural mortality rate would tend to fluctuate as a function of fishery intensity and local predation intensity; and overall mortality would depend upon "open site" recolonization related to the number of species and recruiting individuals competing for the "sites". This involves extremely complex feedback loops. It might well be more useful to assume that reef fishes of various habitats have tended to achieve similar growth and recruitment potential, and that knowledge of size-age structures and substrate area might actually give the best estimates of turnover rates, hence fishery potential in these cases.

BUILDING THE "UNDERSTANDING MODEL"

A numerical model is nothing else then a representation of an "understanding model" in the sense that it simulates and integrates our knowledge on the modelled processes. It will take into account the available facts and put in equation the hypotheses put forward in order to explain these facts. It will therefore be just as good or bad as our knowledge was. There is very likely a marine population to fit most conceivable models. We do not believe, however, that there is any single model to fit all fisheries, or that there is an available model for all fisheries.

The common denominators of neritic resources are difficult to identify, although some certainly exist in smaller time-space references. Our problem is that starting with any single resource upon which a fishery develops, how much and what kind of information is necessary to adequately and effectively "manage" both the distribution of fishing effort, and monitor the resource such that the effort appropriately tracks any changes in the resources' distribution, potential, or position in its milieu, the ecosystem?

This is not a simple question and there is no simple answer. The elements need to be examined in perspective, leaving only specific examples of individual species aside so as not to clutter the discussion with anecdotal material.

There is a fairly extensive historical log of the efforts of scientists (and philosophers) to unravel the marvels of the sea, e.g., Pliny and Aristotle's writings; the studies of Linneaus; and records of the age of exploration of the seas, culminating in Darwin's treatise on speciation. Astute marine biologists flowered at the turn of the twentieth century. Early insights of the Norwegians were documented by Hjort in his treatise of 1913-1914, and Graham's (1935) development of fishery statistics and continuing efforts to understand environmental effects of feeding, growth, maturation and early life history of fish are remarkable. It seems that few of us today have progressed beyond their insights. Of course, there have been remarkable re-developments of basic concepts, and subtle mathematical expressions devised to express them, but the problem of obtaining better insights into what causes the variations and how to cope with them has not been resolved, although we may be getting closer in solving some of the intermediate questions.

Early pioneers in fishery-oceanography like Kishinouye (1923) and Uda (1927, 1952) had already formulated relations between, for example, species morphology, physiological capabilities and oceanic variations, hence zoogeographic and fishery related behaviour. The importance of system variables, currents, temperatures, oxygen, food abundance, etc., although certainly recognized, have too often been taken in gross forms, i.e., average surface temperatures for a series of months, and these values have been "regressed" or "correlated" with fishery yields or recruitment. Short series containing correlated trends have been identified for numerous data pairs. Skud (1982; this volume) has also pointed out that they actually reverse under certain conditions, usually involving a change in dominance of one species with another, and the second species often takes on the response pattern characteristics of the first species upon which the correlations were based. This speaks clearly for opportunism in the face of a system-wide change of state.

Meanwhile, it is also important to recognize early on that fish are very much part of a larger system, loosely termed an ecosystem, which they, in turn, support various components of, and from which they extract their needs. The ecosystem is constituted of intrinsic (internal) components, and extrinsic ones. Time and distance scales are very significant in interpreting changes in the fishery catches, particularly as they might reflect effects of factors extrinsic to specific fishery geographies. Fisheries do not reflect only local events, but also climate-ocean and solar system driven changes, which induce biological ones. It is important to realize that within even these ecosystem constraints the basis of all present modelling of populations is the "unit stock" assumption for each resource under study. Eventually, the questions arising from observed variations must be addressed with regard to any potential non-homogeneity, or non-uniformity arising from sub-population level components. This should be the starting place for modelling resources, but usually is lost in the manner of most assumptions.

In the following sections some of the key difficulties encountered when trying to build our understanding model of exploited fish population will be discussed, starting by the basic problem of collecting information on the population/sampling problems. The concept of unit stock will be relatively extensively discussed because of its overwhelming importance in modelling. It will be followed by a discussion on the use of CPUE as a measure of abundance in schooling fishes.

The two last sections of this chapter will deal, through illustrative examples on larval survival and stock-recruitment relationships, with the problems of causality and hypotheses structuring on the one hand, and of preconception of results on the other hand, both processes leading to slower progress in understanding and therefore in realistic modelling of exploited populations.

Sampling Problems

Sampling the Sea

Since the advent of the age of exploration of the seas there have been relatively few innovations in biological sampling of the sea. We still use filtering, via towed nets, as a primary sampling tool, with some relatively recent advances made on how to capture more synoptic time-space frames from relatively controlled monitorable devices such as the Batfish (Dessurault, 1976) or Undulating Oceanographic Recorder (Aiken, 1981) for fine (meter) scale resolution; BIONESS (Sameoto et al., 1980) and the Longhurst-Hardy Plankton Recorder (Longhurst and Williams, 1976) for slightly increased scales; and the standard arrays of plankton nets for larger, more integrative scales (see Fasham, 1978 for review of net sampling scales and their resolution limitations). For studying larger, mobile species we are still pretty well limited to fishing gear or experimental versions of these.

On the other hand, the physical oceanographers and climatologists have taken advantage of the increased technologies of the electronics industry by deploying deep sea pressure-tolerant encasements, buoy suspended or free floating (e.g. SOFAR) gear, as well as airborne or satellite-borne sensing and information transmitting technologies. This has allowed them to obtain synoptic measurements with deeper as well as broader temporal and spatial resolution of the seas. Biological sampling is still in very primitive condition in contrast, although even the satellite-scanners can yield rather important information on fronts and eddies, phytoplankton distribution patterns, etc. (Pingree, Holligan and Mardell, 1978). The fishery resources are simply unresolvable with present techniques. Such contrasts in technology must some way be diminished if fishery biology is ever to fully mature into anything beyond empiricism and anecdotal time series. The major point being that the improvements in sampling and monitoring technology have not been parallel in the various realms of ocean research.

Recent attempts to employ high frequency sonar scanning technology for monitoring the plankton and calibrate these signals with multiple sample plankton nets showed that the daytime signal variations were due to large copepods and small euphausiids, while at night the signals indicated changing small fish, squid and larger euphausiids (Greenblatt, 1982). Patchiness in these signals differed very little diurnally, but the patch contents were indeed different. The importance of collaborative sampling in contrast to total reliance on any one technique is evident. Any proxy technique will need continuous "subsampling" and calibration in order to be useful in studying resource behaviour.

Sampling of Fisheries

A major problem in approach to fishery resources compared with terrestrial populations is that fisheries can only rarely sample in an unbiased manner the populations upon which they operate. Size-age, migrational, and other stratum limitations confound the basic sampling which the fishery scientists must again subsample in order to draw inferences. Figure 3 from Caddy (1983) shows the effective differences between various fishing gears in a Caribbean reef fishing area. However, it is still necessary and possible to study and draw inferences from these catches, and their associated fishing efforts, provided each element is accounted for. From studies of size (length and weight) and age we can obtain growth estimates. From sampling length frequencies in catches we can infer age structure, i.e. relative abundance by size-age. From a time series of these we can begin estimating total mortality (Z), and estimating natural mortality (M) and fishing mortality (F).

Through various methods, some employing fishery statistics, others utilizing independent survey methods, biomass estimates are obtained, along with age structure data. Time series of these data can give estimates of numbers of individuals at different ages or sizes and then estimates of recruitment, mortalities and effective fishing mortality can be made. The availability and accessability of these data have lead fisheries scientists to look into the yield-per-recruit (Y/R) relations and stock-recruitment (S/R) or dependency between adult biomass and subsequent recruitment.

The problems of fishery scientists do not end here, and in fact, have proven to often begin once these data are available and their analytical results are in hand. What is usual is that every parameter is found to vary such that it becomes impossible to pinpoint with reasonable accuracy just which variables are responsible for observed variations in age distribution, catch rates, or total biomass of a resource from these data.

For most fisheries, research has evolved to include fairly precise descriptions of the fishing effort itself, through log books for example, such that the distribution of effort, catches, size-age groups are recorded. This step, it appears, is very important to even cursory understanding of any variations in the catch statistics, as we will see.

Stock Concepts

The objective of the following discussion is to review the stock concept, definition, and applications in fishery management.

Various stock characterization techniques and their relative merits and weaknesses are reviewed and these are summarized in table 2 for ready reference.

Recently Booke (1981) defined the word stock for the Stock Concept International Symposium for application in fishery science. The general definition (i.e. vague) he gave was that "a stock is a species group, or population of fish that maintains and sustains itself over time in a definable area. In a more precise manner, stock can be defined, where genotype is known, as a population of fish maintaining and sustaining Castle-Hardy-Weinberg equilibrium. Where no genetic basis is available for characterizing a stock, then phenotypic definitions need to be recognized so that a population of fish would maintain these characteristics and therefore could be called a stock".

The latter case is the one generally applied today. Booke also emphasizes the need to recognize stock genetic variability and measures of it in management, given the guardianship implication of fishery management.

Probably more familiar to the usual stock assessment community is the assignment of stock labels by convention, based on fishing gear, geography, i.e., ocean hemisphere, or simple species designations, i.e., South Atlantic albacore, Baltic herring, etc. The numerous very tenuous stock structure hypotheses for most fish species have tended toward hemispheric or large regional approaches to stock definition.

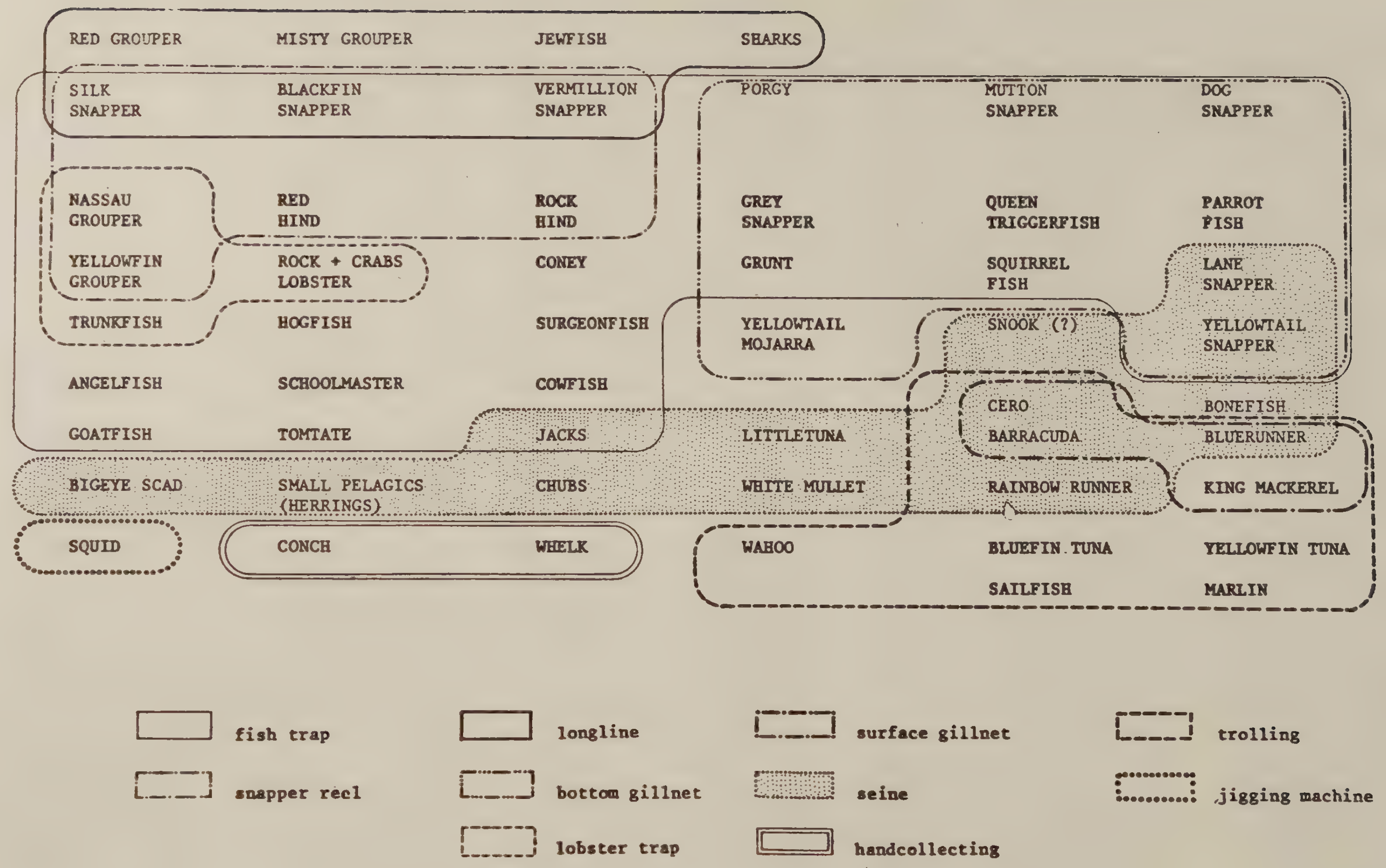

RED GROUPER
MISTY GROUPER
JEWFISH
SHARKS
SILK SNAPPER
BLACKFIN SNAPPER
VERMILLION SNAPPER
PORGY
MUTTON SNAPPER
DOG SNAPPER
NASSAU GROUPER
RED HIND
ROCK HIND
GREY SNAPPER
QUEEN TRIGGERFISH
PARROT FISH
YELLOWFIN GROUPER
ROCK + CRABS LOBSTER
CONEY
GRUNT
SQUIRREL FISH
LANE SNAPPER
TRUNKFISH
HOGFISH
SURGEONFISH
YELLOWTAIL MOJARRA
SNOOK (?)
YELLOWTAIL SNAPPER
ANGELFISH
SCHOOLMASTER
COWFISH
CERO
BONEFISH
GOATFISH
TOMTATE
JACKS
LITTLETUNA
BARRACUDA
BLUERUNNER
BIGEYE SCAD
SMALL PELAGICS (HERRINGS)
CHUBS
WHITE MULLET
RAINBOW RUNNER
KING MACKEREL
SQUID
CONCH
WHELK
WAHOO
BLUEFIN TUNA
YELLOWFIN TUNA
SAILFISH
MARLIN
fish trap
longline
surface gillnet
trolling
snapper reel
bottom gillnet
seine
jigging machine
lobster trap
handcollecting

Fig. 3. Species classified by availability to gear. (From Caddy 1983).

Table 2: Methods, utility and data sampling characteristics for population discrimination.

Technique	Method	Relative unit cost	Data Type	Determination of population characteristics	Definitive or not in discrimination	Weaknesses and Strengths	
^{A1}Protein characterization	a. electrophoresis	low	non-parametric	sample size dependent	yes	sampling difficult	genetic basis
	b. electrofocusing	high	non-parametric	sample size dependent	yes	procedure slow	highest resolution
	c. purification and functional analysis	very high	parametric	sample size dependent	can be	technique difficult	great sensitivity
^{A2}Chromosomal comparisons	a. karyotyping	low	subjective	can be useful	can be	requires big differences	genetic basis
	b. banding studies	moderate	subjective	can be useful	yes	requires large chromosomes	genetic basis
^{A3}Mitochondrial DNA	a. isolation and fractionation	moderate	non-parametric	sample size dependent	can be for familial studies or differentiation by area	tedious procedures	maternally inherited
^{A4}Color patterns	a. pigmentation patterns	low	non-parametric	can be useful	can be	basis needs determined i.e. ontogenetic or hereditary	usually genetic basis
^{A5}Immunology	a. tissue typing, i.e. blood	low	non-parametric	sample size dependent	yes	sensitive to ambient	genetic basis
	b. microcomplement fixation	moderate	non-parametric	too sensitive	yes	very sensitive	species level tool
^{A6}Numerical or Metrification studies	a. hard part dimensions	low	parametric	can be useful	yes	basis needs determined samples must have common expectation	usually regionally specific, often genetic basis
	b. morphometrics of body dimensions	low	parametric	can be useful	can be		
^{B1}Growth and life history parameters	a. age-growth by 1. annual ring on hard parts.	can be high	parametric	often useful	corroborative	subjective	ease of collection
	2. daily growth rate	high	parametric	definitive	can be useful	needs calibration	gives rates on short term basis
	3. tagging-recovery	high	estimation	not usually	corroborative	usually biases in release and capture	tagging changes natural patterns on short term
	b. onset of maturity	low	parametric	useful	corroborative	differences can be induced by environmental changes, difficult to evaluate true number of eggs produced or hatched	helpful in assessing changes - often less important than the knowledge of where eggs are successful
	c. fecundity	moderate	parametric	useful	corroborative		
^{B2}Distribution studies	a. mark and recapture 1. tags and markers	high	point A to B	can be useful	corroborative	needs substantive support data of A type	fraught with estimation errors but useful for assessing movements
	2. hooks	low	point A to B	can be useful	corroborative		
B3 Natural tags	a. parasites	moderate	non-parametric	can be useful	corroborative	can be lost or transferred	area/host specific
	b. chemical/hard parts	high	parametric	can be useful	corroborative	can be transferred or source can be spuriously distributed i.e. currents	high information if source specifically located
^{B4}Meristic counts	c. gillrakers or vertebrae	moderate	parametric	not useful in tunas	no	highly variable in some species due to ambient	can indicate some species differences.

Applications of Stock Concepts and the Underlying Causality Problem

The simple panmixis hypothesis, welded together with the assumption of constant or average parameters in fishery models has led to the long-term failure of "conventional" fishery stock assessment and management procedures in many species, including tunas, and has retarded applied ecology in general. The common denominator is a logical error inherent to the assumed simple stock hypothesis.

"Use of average parameters is non-conservative during times of population stress".

Although a mathematical average will always be obtainable from a sample, that "average" individual or condition may not exist at any specific moment. This is the essence of the problems with application of mathematical theory and the theories of population genetics, evolution, and ecology as a subset of general biological science. Also there are few environmental characteristics which can be shown to be constant, or near "average" more than two short periods every year or so.

"Evolution of individuals, species and systems are continuous, i.e. progressive."

As a starting point in delineating "stocks" it should be obvious that the geographic location of reproduction is an important criterion, but that species may have variable geographic and temporally stratified reproduction, sustaining more complex rather than simple panmictic populations within any geographic context. These complex age-structures imply complex temporal and spatial patterns of reproduction.

The recent advances in thinking regarding marine teleost larval fish requirements (Hunter, 1980; Lasker, 1975; Sharp, 1981a, 1981b) have provided considerable basis for changing the usual premises applied to fish reproductive success. The concept of a "survival window" in time and space, arising from studies of the critical energetic requirements of larval fishes and the processes which promote them, is the key to better understanding the multiple cohorts of recruits entering most fisheries.

If we start with the basic premise that it takes nutrients to sustain marine life, and "new" nutrients to either sustain or increase biomass, then clearly one needs to examine the basis of nutrient sources and their availability to larval fishes, and their eventual conversion to biomass in various forms. These are processes determined by energy input and form, i.e. light, turbulence, terrigenic and biogenic nutrients, etc. Starting with photosynthesis, by definition driven by light, the presence of nutrients, and catalysts in the form of organisms, it provides the initial hierarchic step in a long chain of energy transfer and transformation leading up to fishable resources. The larvae must be placed into the appropriate milieu (Sharp, 1981a, 1981b). Until they transform into mobile post-larval stages they are directly influenced by local physical and density dependent requirements in regard to their food sources.

The necessary conditions are not universally or evenly distributed so that each larval group or "cohort" is the evidence for a "survival window" which generated the opportunity for their successful development. That proportion of eggs sown into the sea which will encounter the appropriate conditions, i.e. high food availability and low predator abundance, must be highly variable and likely accounts for the absence of a clear relation between adult biomass and subsequent recruitment in most fishes, but particularly in the nomadic species such as tunas and other oceanic species.

The numerous species of scombrids and their diverse distributions is a clear indication of the complexity of their habitats. The evidence from even cosmopolitan species, like yellowfin and skipjack tuna, supports a localization and differentiation hypothesis for population structures (Sharp,1983; Richardson,in press). The relative amounts of mixing of population components in various regions very likely accounts for the differences in relative abundance and productivity among regions, and in seasonal and annual patterns of vulnerability to various forms of fishing. Many species are fished during or just prior to their reproduction aggregation. In these instances stock structure studies may be unimportant. However, many species have less well defined reproductive behaviour, and better understanding is required.

The problems of oceanic species compared with neritic species are worth considering before proceeding on to techniques for discriminating populations. For example, the major difficulty with obtaining any rigorous kind of stock identification of or labelling device for tunas is the very cryptic nature of their reproduction. For most tunas we have little or no knowledge of the relation between those individuals recruited to the various fisheries, the adults in major ocean areas and the eggs, larvae and prerecruitment juveniles.

So far in the world's tuna fisheries we have only a few examples where less than 40 cm (or 9-12 month) fish are abundant in commercial catches. The Philippine payao fisheries yield abundances of small skipjack, yellowfin tuna and occasional bigeye, as do the surface fisheries for tunas in the Gulf of Guinea and West Africa. Occasionally similar phenomena are observed in the transition zones in the eastern Pacific Ocean fisheries.

Although there is little evidence for or against localization or very small population ranges in the genus *Thunnus*, or for the Thunnini in general, it is likely that the smaller, less mobile stages are indeed more influenced by "local", i.e. metre to kilometre scale, current or water mass phenomena, whereas the 10 cm and greater stages become more and more independent of these "local" features of turbulence, eddies and advection (Sharp, 1981b).

Nakamura (1969) published his anecdotal correlations between apparent abundance, as measured primarily by longline catch and effort, and the current and/or water mass structures. Given this basis, in light of the studies of Saito (1973; 1975) Hanamoto (1975) and Suzuki and Kume (1982), as well as the improved understanding about the physiological ecology of tunas (Sharp and Dizon, 1978; Sund et al., 1981) it is moot that the physical environment heirarchically molds or forms the potential for all fisheries, particularly tuna fisheries. These processes are neither mystical nor particularly untenable, given that one does not expect to predict, sensu strictu, the presence and abundance of fishes in the ocean. The manifold solutions to environmental and ecological challenges to biological persistence are met in the sea by the behavioural and physiological plasticity within and among species.

Except for a few areas, the year to year catch variations for tropical tunas are on the order of 1 to 5 times, low to high, with smaller geographic reference areas exhibiting variations of the order of 20 x, or more (Sharp, 1981b). The relative independence of the larger tunas from local ambient conditions due to their high mobilities can be used to explain some of this variation, the rest is tied up in population structure, component mixing and density dependent schooling dynamics (Sharp, 1978; Sharp MS - What is a tuna school?). To ignore these processes is to ignore the basic tenets of biology, and evolutionary processes.

Other species, as are documented throughout this consultation undergo similar and even greater year to year abundance changes.

To expect less than continuous, slow changes in ecological systems is to be unaware of normal system variations in both ambient energy-nutrient fluxes and subsequent biological responses. These happen on both long and short time scales, affecting local and wider areas. Stock assessment in most cases is still based upon equilibrium states which are not only unlikely, but also misleading. The stock concepts have evolved around this equilibrium assumption and can hardly cope with the processes evident in today's fisheries, i.e., the numerous blooms and recolonizations by species for which we have records of previous fisheries, or the new development of fisheries in areas where these have not been observed before.

In fisheries where fleets are mobile and catch variations are minimal, there is an inherent urge to assume stability of the underlying resource, i.e. unit stock. What this can often be attributed to is that the "stability" is an artifact of "too broad" a definition of the unit stock. In fact the underlying genetic units may indeed be sequentially decimated, without signals from the catch statistics.

Given that speciation is an extreme form of population differentiation in response to environmental changes, the lesser scales of changes and characterization of these processes within a species needs to be understood before a useful stock concept can be clearly defined.

Population Variation and Characterization

The individuals of a given species are the fundamental units of biological evolutionarily significant selection. The low fecundity species such as mammals have little chance of having identity in chromosomal-gene level structures, or their expressions. This, and the effects of differing environments produces the nearly infinite array of effects and characteristics in even closely related individuals. Fishes, with superior fecundities, and facing quite extreme selection, have evolved a more near uniformity in many cases, but individuals are still usually distinguishable, if enough characteristics are examined.

The most recent survey methodologies applied to characterization of the genetics of species, which are considered to be relatively sensitive, hence definitive, are:

A. 1. Protein or enzyme characteristics
   2. Chromosomal comparisons
   3. Mitochondrial DNA comparisons
   4. Color patterns
   5. Immunological reactions
   6. Numerical or metrification studies

Methods 1, 3, and 5 are quite discrete and can be categorized as being useful for both differentiation and consolidation of identities. Methods 2, 4, and 6 are fraught with subjectivity and integrative, hence less definitive, except for differentiation, where they are adequate inferential tools.

Another list of inferential tools can be constructed which permit various levels of inference to be made, but which alone cannot be definitive. Unless far more data are collected or spawning populations and/or heritability are known and studied extensively, their uses are primarily for estimation, but all population structure conclusions based only on these data are tenuous.

B. 1. Growth and life history parameters
   2. Distribution studies through mark and recapture
   3. Natural tags
   4. Meristic counts

Because this important domain of knowledge is often only partially available to classical fishery biologists, a short series of discussions of each kind of data is given in the Annex 1 on stock characterization.

Catch per Unit of Effort and Abundance

Effort distribution in relation to the resource distribution, availability and vulnerability needs to be carefully evaluated before fishery data are informative, i.e. interpretable. This usually implies that fishery independent sampling has been initiated (e.g. research programmes or fishery monitoring programmes). The difficulty is to know the true distribution of the resource population, and monitoring this single parameter may tell more about the status of resources than most other statistics.

The first of many sampling problems in fishery research is, therefore, to determine the distribution properties of the subject resource. The aggregations of resources in marine environment are complicated by the three dimensional, highly dynamic transport properties of the water column, seasonal distribution discontinuities and the behaviour of the size-age groups in a population. If the "recruits" to a fishery school, or the aggregate for spawning are diffuse, yet contagiously distributed, sampling interpretations change. Of course, the vulnerability of fish, particularly schooling fishes, can vary tremendously in time and space, in response to numerous variables. Since this is the case, tremendous biases can and do result from fisheries sampling these populations. To try to portray the numerous variables in this complex of interactions it should first be recognized that there is a distinction between available resources and vulnerable resources.

The available resource comprises the whole, finite, abundance of the resource, including all recruited individuals. The space frame of the available resource is the total area or volume inhabited by the resource. Depending on the distribution and migration pattern of the subject species and the space constraints of the fisheries, we may find that only a portion of the available resource will occur within the range of the commercial fleet or gear being used. The combination of these two characteristics will define the accessibility of the resource to the given fisheries. Furthermore, only part of the individuals will be vulnerable to specific fishing gear, and will be subject to being caught, either because they are found in relatively big schools, are ready to bite, or show low mobility. For instance, most neritic fishes will be accessible to almost any type of pelagic fisheries provided they are reasonably close to the surface and within reasonable navigational distance from a fishing port, but they will only be vulnerable to purse seine fishing if they are part of a commercial size school. In the simple catch equation

$$C = qf\overline{P} \qquad (1)$$

q is the purveyor of this information. This coefficient can be broken into gear (man), behavioural (biological) and physical (environmental) components which yield perhaps the most dynamic aspects of this simple view (equation 1) of how fisheries operate. Whereas in the past the catchability coefficient (q) has been held "constant" in deference to the nearly measurable C and f parameters so as to determine P; in a number of cases it has become clear that this "convenient" approach can lead to erroneous interpretations (Garrod, 1964; Paloheimo and Dickie, 1964; Clark, 1974; Pope and Garrod, 1975; Francis 1977; Sharp, 1976, 1978, 1979; Clark and Mangel, 1979; Csirke, 1980; Pope, 1980) and a non-useful approach as to the evaluation of the dynamic aspects of both fisheries and schooling resource populations.

While it is fascinating to consider the variability of each of the coefficients in the simple catch equation, it is more important to consider the sources of the variation. What is measured in a typical fishery is the total catch (C) and the fishing effort (f). The total catch has errors in the 5-20% range depending on reporting, species identification, and proportion of the fish entering controlled markets and fishing effort, has all the associated uncertainties of the catch composition plus a number of other sources of errors related to changes in efficiency, technological improvements, learning changes in target species, etc., which vary widely from one fishery to another.

A list of the variables contributing to C as implied from the three variables q, f and P are given below with contributing variable properties following each parameter.

P, population size, is characterized by

1. Age structure
2. Geographic distribution by size-age
3. Differential ecological interactions by size-age
4. Differential potential for reproduction by size-age

f, the effective effort varies with:

1. Gear type (hooks/day; bait utilized; mesh size; etc.)
2. Relative efficiency (functions of saturation, effectiveness, etc., position on learning curve of gear, competition or interference of effort, etc.)
3. Distribution of effort over the resource range

q, the catchability coefficient is a "fudge factor" affected by:

1. Availability (function of P_2 and P_3)
2. Vulnerability (function of biological properties and ambient properties in relation to f_1 and f_2)

The biological properties having a direct impact on CPUE as a measure of abundance are:

a) schooling or aggregating behaviour

b) willingness to "bite" bait or to "stay put" for gear effectiveness

c) seasonal density dependence of P_2

The ambient properties affecting CPUE are:

a) sea state, visibility of cues, gear appropriateness, which affects vulnerability of fish

b) depth of limiting features, i.e. thermal, oxygen profiles, bottom topography, etc., which affects habitat size of the available resource and

c) proportion of local population drawn or concentrated into area where fishery is located, i.e. accessibility

Until most properties of these parameters are understood, we will not have enough understanding to explain the variations in catch, relative to effort or any other parameters with sufficient confidence to consider the standard management options a variable resource will offer.

The environmental dependences of variations in q are quite well evidenced in the tuna fisheries of the world. A complete description exists for surface gears, particularly purse seine operations on "school fish" (Sharp, 1978, 1979). Francis (1977) examined q variation in the eastern Pacific Ocean yellowfin purse seine fishery with respect to size recruitment period (semestral groups), geography (nearshore to offshore) for "average" annual data. His table 2 (page 241) shows that there are marked differences between "catchabilities" of tunas by size in the three areas, up to 20 times the "average" annual data. Given this "smoothing procedure" one could expect at least five times this variation in the individual area annual values, and perhaps several orders of magnitude more from monthly, inter-annual evaluations. Total catch varies on the order of percentages from year to year, local catch varies by orders of magnitude from year to year. Fishing effort varies only in quality and location. This is not unique, but an example of the variations to be expected in schooling fishes.

It appears that many of the problems inherent to the interpretation of fishery data are the result of extrapolation and integration of data beyond their limits of representation. Assumptions are necessary, but their appropriateness, rather than their convenience should be the first consideration. Clearly fishing effort on schooling species is operational only because the fish aggregate. These aggregations have finite distributions or ranges, which vary considerably among species and size age groupings within species. The units of effort are simple predator analogues, which are effective only when a school or an aggregation of schools is behaving appropriately so as to become vulnerable to the gear employed. These schools are not the basic units of the underlying population in most cases, but composites of what are described as core units (Sharp, 1978) or elementary populations (Lebedev, 1970). The study of the properties of these fundamental building blocks which must converge, merge and redistribute themselves to varying degrees is not part of the "conventional wisdom" of population dynamics, but some believe it holds the key to many important questions.

Clark and Mangel (1979) have given a preliminary description of the Michaelis-Menten, enzyme-substrate analogue models which we feel best represents the important "schooling" dynamics. Their proposed models have definite limitations in application, due primarily to our ignorance of the effects of 1) density dependent schooling dynamics, 2) distances over which the attractions between aggregators and schools operate, (3) size specific behaviour of schooling fishes with respect to same species and multispecies aggregations and 4) the distribution properties of the size similar, core schools which are the building blocks of the underlying population fished by the various gears. The important questions are the dynamic ones, but a fundamental basis for our understanding of these depends more on the validity of the "core school" concept.

Fishes with some dispersion in their occurrences provide even more intriguing problems, particularly if their habitat of life history includes a gradient in vulnerability and a substantial portion of the resource can be considered to have a "refuge" against fishing effort, i.e., *Trachurus* species in the Eastern Boundary Currents, some flatfishes, oceanic species, etc. Other examples are species associated with kelp beds or rock piles, where usual trawling effort is not effective or practical. What is needed is some estimate of "recruitment" to and from the refuge. The problem is that sampling and monitoring is far more complex than a "normal" fishery sampling programme can provide for, hence we can lose track of substantial population elements. This phenomenon could account for a large amount of unexplained "stability" of some resources in the face of intense exploitation.

Fishery resources can be found in innumerable distribution patterns, from windrows (i.e. invertebrates) to schools on through relatively uniform dispersion over a habitat. It does not matter so much which pattern is prevalent, as long as it is known to some degree. Schooling fishes are often aggregated in density dependent, size (length) determined groups, usually with a negative binomial aggregate-size frequency. Fisheries select for intermediate to large schools for obvious reasons, and this confounds interpretation of catch and effort related statistics. The distribution frequencies of individual schools would better reflect local abundance of density than the integral catch rate statistics, except when a resource is very disperse (i.e. not aggregated). Only careful records of time and space related catches (e.g. via precise logbook reports) can help one interpret such interactions.

Causality and Hypotheses Structuring in Larval Survival

Continuous studies have sought to close one of the most important gaps in fishery science, the one which stands between a cohort of fertilized eggs' entry into the sea and the recruitment of the subsequent group of fish at some later date to fisheries. The problem hinges around the observation that some 5 to 6 orders of magnitude losses are realized during this period, and usually estimates of year to year recruitment variation for natural, not heavily exploited fish populations range from about 2 or 3 x to about 500 x or about 2.5 orders of magnitude (Ursin,1982; Hennemuth, Palmer, and Brown, 1980). Ursin's (1982) discussion of the relative stability of ecosystems suggests that even this variation is small compared to what might be expected unless there are considerable stabilizing influences.

Rosenthal (1970), Jones (1973) and Lasker (1975; 1978) have each rediscovered the early life history as the most sensitive period, as proposed by John Hjort in 1913-1914. The modelling studies of Vlymen (1974; 1977), Beyer (1980) and Beyer and Laurence (1981) provoke one to consider that spatial distribution and quality of esculent particles in nature control the first in a sequence of hierarchic hurdles to be cleared if any larval fish is to survive to reproduction ages (Sharp 1981a).

While theory, modelling and restructuring of research plans and activities have taken some years, recent reports (O'Connell 1980) and research in progress (Theilacker, personal communication) have given adequate support to this concept that to ignore it is futile. Likewise the importance of predation cannot be in any way ignored, as clearly natural mortality is either due to direct or secondary predation ($M = M_{p1} + M_{p2}$). The problems of monitoring directly either M_{p1} or M_{p2} are formidable, and to-date are not well documented for larval fishes in nature except by inference (Alvariño 1980). Sampling post-larval pelagic fishes is sufficiently difficult that quantitative studies of distributions and abundances are nearly non-existent. Demersal post-larvae of some species are somewhat less difficult to sample, and Zijlstra, Dapper and Witte (1982) offer again remarkable insights into variations in growth, mortality and early life history related density dependent processes for one demersal species.

Meanwhile other researchers (Owen 1981, Mackas and Boyd, 1979; Sameoto 1981, Smith et al., 1981, and Coombs et al., this volume) are finding that the stratification and densities of organisms, larval fish food particles and larval fishes are indeed related on scales predictable from models and laboratory physiology and behaviour studies. These studies are the necessary logical feedback into the restructuring of research programmes and continue to add fuel to the efforts of climate-ocean researchers to find linked cause-and-effect relations between climate-weather-ocean variability and subsequent larval and small juvenile fish survival (Bakun and Parrish 1981, Bakun et al., 1982, Parrish et al., this volume).

Platt and Denman (1975) have given a fair representation of the expected biomass spectrum (particle size frequency), and a good example of a "bolus" of energy passing upward through this spectrum. The point that needs considered is that the distribution of volume densities (contagion) are greatly affected by the negative binomial distribution at each and any size range, i.e. it takes several orders of magnitude more individuals of 50-200 ym_x phytoplankters to reach a mass equivalent of even a fish larva, but we only rarely observe via sampling naturally occurring densities of phytoplankters of this size range in sufficent relative abundance or concentration to support feeding fish larvae (e.g. 0.8 to 3.0 times the larval fish biomass per day, depending upon species, temperature, and activity of the larva).

The concept which is often neglected is that where the lower densities prevail, none of the predators in the milieu can operate in a positive energy balance. This leads one to reason that larger individuals need to be mobile in order to survive, and that the smaller predators, i.e. fish larvae, must either be situated in or very near appropriate densities or they will indeed starve, and become subject to predation (Sharp 1981b).

Simpler, single cell organisms have evolved stasis mechanisms such as encystment and dormant phases which preadapt them to nutrient poverty periods of relatively long duration. Settling out of the upper water column, into cooler waters, slows basic metabolism to some degree, but to be successful, i.e. persist and reproduce, single cell organisms or small predators must either be transported or swim upward into photic, productive waters again, or be able to somehow persist on the rain of detritus and debilitated organisms from above. Those that cannot will themselves become detritus.

Since it is also certain that nutrient and particle injection into the photic zone that is sufficient to stimulate primary productivity is neither uniformly nor stochastically distributed in regard to location, timing or amount, then it is nearly certain that the sequential processes of colonization, predation, growth and reproduction by each oviparous fish species contains a series of low frequency-of-occurrence requirements which cannot be attributed _a priori_ probabilities or even averages. Hence stochastic, process models might only be _useful_ to represent _known_ distributions and occurrences. This also implies that only causal ecological _modelling_ based on directly linked processes or localized interactions can be expected to be predictive in any realistic sense. Probabilities of interaction are therefore, only interesting on very small scales, i.e., meters/minutes (see Vlymen 1977), whereas above these scales they approach zero very rapidly. The only reprieve in this case is the increased mobility of larger predators which expands the probabilities of interactions over larger scales, i.e., km-days, between larval fishes and their more mobile predators. However, as the larvae develop, their numbers decrease and even though total biomass goes up, their tendency to aggregate also increases, decreasing a predator's opportunity to encounter them. (Further evidence that this is a problem is the fact that the first schooling phases and their predators are poorly known for most marine fishes due to their infrequent occurrences and patchy distributions (Hewitt 1982, Smith _et al_., this volume). This decimation and biomass increase is an ever upward _spiralling continuum_ which ultimately results in the various observed distribution patterns and characteristics of adult fishery resources, i.e. solitary to schooling, sedentary to highly mobile; abundant to rare; small size to larger size; homing reproduction to opportunistic reproduction; wide distributions; or limited distributions. What is important is that the eggs be placed into sufficiently amicable environments to begin development; that upon hatching they find themselves in the "rare" high density portion of the distributions of their food; that they find themselves in a null or near null abundance of their respective predators; and that they manage to develop rapidly enough to mobile stages, perhaps even to schooling stages, so that they can begin searching for the even rarer abundance distributions of their, now somewhat larger prey.

The picture culminates in the simple realization that the distributions of all the lower trophic components are discontinuous, that these species are characteristically opportunists with high production rates, and that these species have evolved in harmony with discontinuities in the physical environment which promote their regular, i.e. serial bursts of productivity, hence persistence.

It is certain that monitoring only larval fish distributions and food particle stratification/destratification processes will not be adequate to allow complete explanations of recruitment in any "larger" system today. However, it is also certain that unless these basic measurements are included in the data proposed to monitor or explain recruitment, there can be no progress. The predator-prey research and technology for sampling post-larval and juvenile fishes up through about 5-20 cm lengths needs a lot of improvement before the complete logical bridge is made between eggs and recruits to fisheries. Methods for measuring organism size distributions in relatively large volumes of open ocean need to be developed so that eventually any major effects of harvests by man or major predation might be measured. It appears that in spite of our zealous efforts to understand the spectrum of fishery resources above "recruitment" sizes, the most biologically important and dynamic changes all occur well below this threshold, while these changes may well be influenced by climate-ocean phenomena many thousands of kilometres and months to years away.

Preconceived Results In Stock-Recruitment Relationships

Perhaps the most common difficulty in which fisheries scientists find themselves when trying to apply their knowledge to fishery data, in contexts of available tools and methodologies, is how much data can or should be "averaged" or integrated to adequately represent a resource. For example, the simple portrayal of Population Fecundity (viable egg production) in any given year and potential recruitment resulting sometime later usually takes the form of a table of figures as shown below:

Year	Estimated total eggs produced	Resulting recruits in year (+n)
t_X	14×10^{13}	8.6×10^6
t_Y	15.5×10^{13}	6.0×10^6
t_Z	22×10^{13}	10.2×10^6
.	.	.
.	.	.
.	.	.
t_N	i	j

A simple plot of j against i for a sequence of years is the usual end point. Some assumptions about a model/form are made and some sort of estimate of the relation between the two estimates is produced. Even less elegant is the use of biomass of adults in the place of total population fecundity, as integrated by use of the biomass figures.

Recent insights about engraulid populations and sequential or iteroparous reproduction shows that for some populations a biomass estimate cannot really be used by itself as an estimate of recruitment potential (Hunter and Goldberg 1980, Parker 1980, Hunter and Macewicz 1980, Alheit *et al*., this volume). Except for a few "homing" populations with precisely determined reproduction periods, it is moot that such attempts to portray potential recruitment are futile exercises.

However, another question can be answered from estimates of egg abundances in the sea. The question is what is the minimum biomass of the females producing the eggs observed? If the data are collected over sufficiently extensive time-area strata to extend beyond the range of reproduction, and if the population is somewhat conservative in its reproduction behaviour, i.e. not too large a variance in either proportions of females spawning, or eggs produced per female biomass, then a reasonable and useful estimate of spawning biomass can be made (Alheit *et al*.; Smith *et al*.; Watanabe; all this volume). It is quite a bit less complex to make these calculations for species with either direct (linear) relations between size-age and eggs produced than it is for a population with allometric fecundity and many size-age classes.

On the other hand, knowledge of *only* the eggs produced will not result in a reasonable "prediction" of the amount of recruits. It is the sequence of events beyond the egg's production and release into the sea which determine this, and these are not events which are uniformly or stochastically occurring (see Kawai and Isibasi, this volume).

The examples provided by Shelton and Armstrong (this volume) on both the anchovy, *Engraulis capensis* and the pilchard, *Sardinops ocellata*, from two fisheries (South Africa and Namibia /Southwest Africa) can be useful in illustrating some of the questions we are trying to address. Figures 4 and 5 show for the pilchard the annual figures for potential spawning biomass and subsequent recruitment. By connecting segmented points starting with the earliest years for which both estimates are available, we have a new insight into the recruitment story. The longest series is that for the South African fishery (1950-1982). The 1950 through 1954 points are clustered about 500-750,000 ton spawning biomass and recruitments are estimated to have been over the range from 8 to 16 x 10^9 individuals. Comparable recruitments occur for the years 1971, 1973, 1974, 1975, 1967 and 1968 when spawning biomasses were relatively stable at about 100,000 tons. Of greatest interest, of course, are the years 1955 to 1962 when the recruitment and subsequent adult biomass bloomed. The surges of recruitment in 1955 to 1957 lead to the adult abundance increases in 1958, 1959 and the 1960 peak of over 1,400,000 tons. Subsequent to 1960 there was a steady decline in both adult abundance and recruitment. While in fact only 1962 recruitment falls within the range of the 1950 to 1954 levels, and from 1963 to 1966 recruitment was quite low but stable, i.e. on a parr with recruitment observed since 1976.

This suggests that the system controlling recruitment went through a sequence of state changes, the earliest ones 1955 to 1957; 1958 to 1960; and 1961 to 1965 where the population size changed dramatically in response to several variables: 1) recruitment enhancement, 2) declining but large recruitment and increased abundance of older age classes due to the previous recruitment, and 3) decreased recruitment as well as senescence and fishing induced biomass declines. Since 1966 the population is small, relatively stable, and the responses of recruitment are obvious. However, the most interesting message in this series is the relatively 'stable' recruitment since 1962-1963. This feature implies that there are "other" limitations on recruitment beyond biomass of spawners.

The sequence of information on the Namibia - Southwest African pilchard fishery is shorter, 1970 to present, but can be contrasted to the situation described in the South African fishery. It would be better if a longer time series were available, but the catch records clearly indicate a northward shift of the abundance of pilchard in response to the massive growth of the population of South African pilchard in 1958-1959. The catches of pilchard peaked in the north in 1968, while the catches were returning to pre-bloom levels (pre-1958) in the south. Clearly the sequence (1970 to present) portrayed in Figure 4 is only part of a complex story in which the sequence preceding it must also have been analogous to that in Figure 3 with a recruitment bloom starting in about 1964-1965, ending in 1967 or 1968 and then arriving at the lower 1970 series of Figure 3.

This set of scenarios compells one to consider that the system-wide patterns of recruitment, from setting adjacent geographic bits together in temporal sequence, to be perhaps the following:

1. While fisheries were developing in both areas from 1950 to 1958, catches stabilized over a narrow, low range.
2. In the south recruitment bloomed in 1955, and resulted in increased subsequent adult biomass, inducing further fishery development.
3. Some of this biomass was displaced northward inducing development of catches in the years 1961 to 1965.
4. In about 1965 the recruitment to the north also bloomed, while in the south it had already declined steadily since 1960 to stable, usual levels in 1962-1963. The population abundance center had shifted north, while resuming usual levels in the south.
5. The recruitment bloom of 1965 in the north lead to shifting effort and abundance hence catches, which peaked in 1968.
6. The population recruitment declined and the fishery and natural senescence induced a decline in adult abundance through 1970, at which time another short pulse of recruitment (1971-1973) once again boosted the abundance, hence catches, and subsequently both northern and southern fisheries have declined due to both low recruitment and fishery induced lowered abundance.

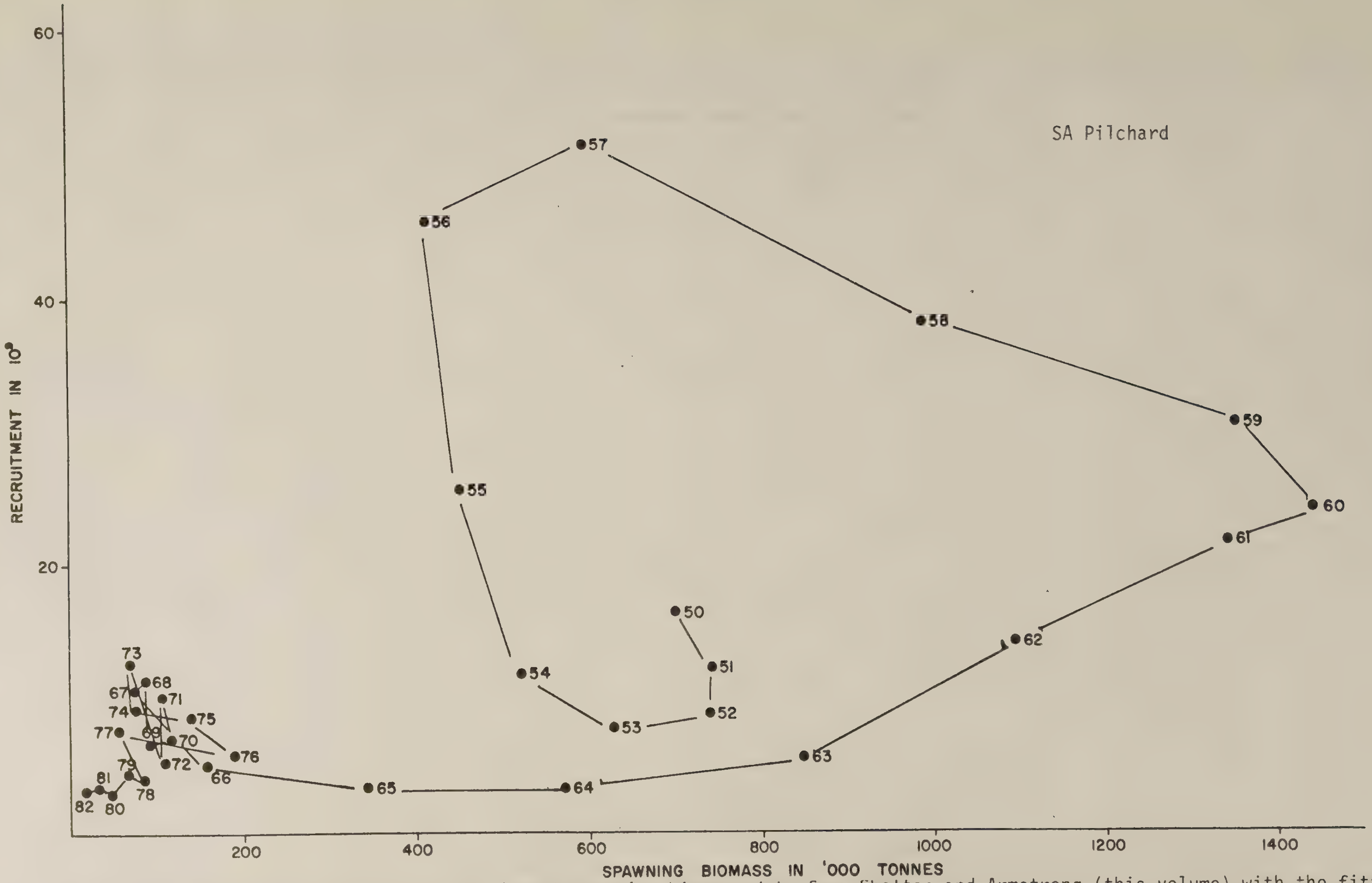


Fig. 4. The South African pilchard recruitment-spawning biomass data from Shelton and Armstrong (this volume) with the fitted curves removed can be quite informative if arrayed in sequence. Note that the entire fishery from 1955 to 1961 was enhanced by a sequence of good recruitment years (1954-1959) while rather more usual levels occurred in 1961-1962, 1971, 1973-1975 and 1967-1968. Poor recruitment does not appear related to spawning biomass, although that biomass certainly reflected previous recruitment success.

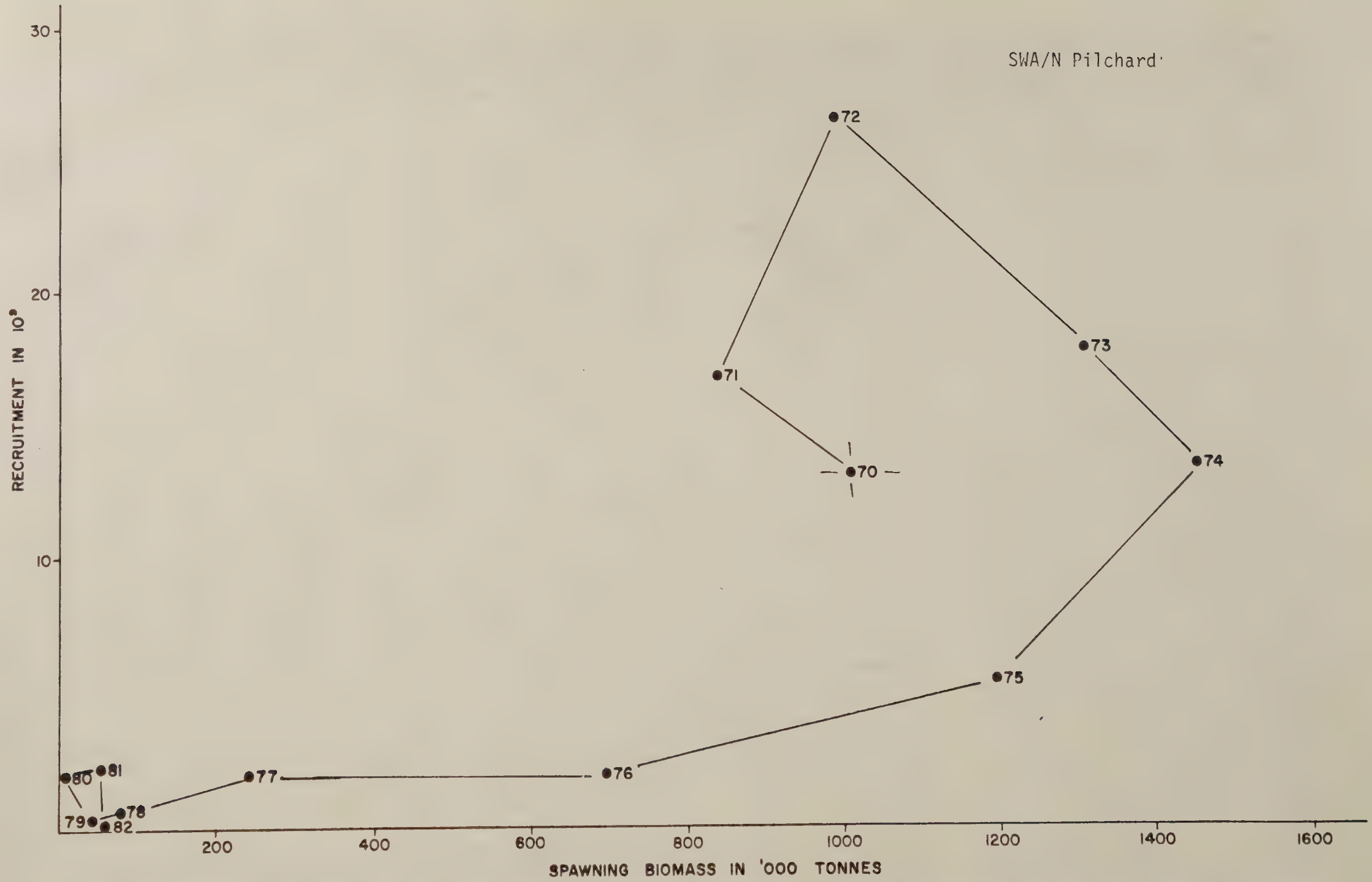


Fig. 5. The Southwest Africa/Namibia pilchard data on recruitment-spawning biomass (from Shelton and Armstrong, this volume) shows a similar spiraling diminish. There is a clear indication that the population density-center changed in the sardine fishery during the years 1960 to 1970, with recent years in both fishing areas being poor since 1975 (see Figure 4 and text).

The anchovy examples are shown in Figures 6 and 7 . The South African anchovy population shows a series of bloom and recession cycles in the period from 1964 to present. A minor bloom is evidenced in 1966 to 1967, a major bloom occurred in 1973, then a series of years of relative stability are observed from 1975 to 1980. In 1982 another major bloom is indicated. All of this is in the face of increased fishery removals.

The Namibia/Southwest African population information sequence is again very short, i.e. 1972 to present, making it difficult to compare directly with the South African information. However, the recruitment has been relatively stable between about 55 and 75 x 10^9 individuals per year over a range of about 100 to 340,000 tons of spawners, with a trend in low years (1976, 1977 and 1979) where lower biomasses yield lower recruitment. In direct contrast with the South African situation, 1982 recruitment is estimated to be very low. Both data sets imply little relationship between adult biomass and recruitment enhancement.

Another useful data series is that from Watanabe (this volume) where he explores the relations between eggs produced in each year, and the eggs subsequently produced by the progeny of that year. Figure 8 shows this pattern for the sequence of years 1951 to 1976 for the common mackerel (*Scomber japonicus*) population of the northwest Pacific. Note the sequences of cyclic blooms and recessions commenced with a bloom observed in the years 1951 through 1963. The first collapse cycle begins in 1964 and by 1968 is complete. The subsequent bloom starts in 1969, from a relatively low production of 200 x 10^{12} eggs, rising steeply in 1970 and 1971 from similar egg production until recruitment to the spawners ensues in 1972 through 1976. The decline in egg production, hence potential recruits begins in 1974 and continues despite high egg production through the end of the series, in 1976.

This double cycle of bloom and recession shows, once again, an independence of implied causality between eggs that generate a given year class and subsequent eggs produced by that year class and in fact shows that these are two periods with entirely unrelated abundance cycles which are more likely due to changes in ambient conditions and distribution than to adult abundance, per se. A feature already demonstrated to be a major cause of variability of recruitment in the Peruvian anchovy by Csirke (1980).

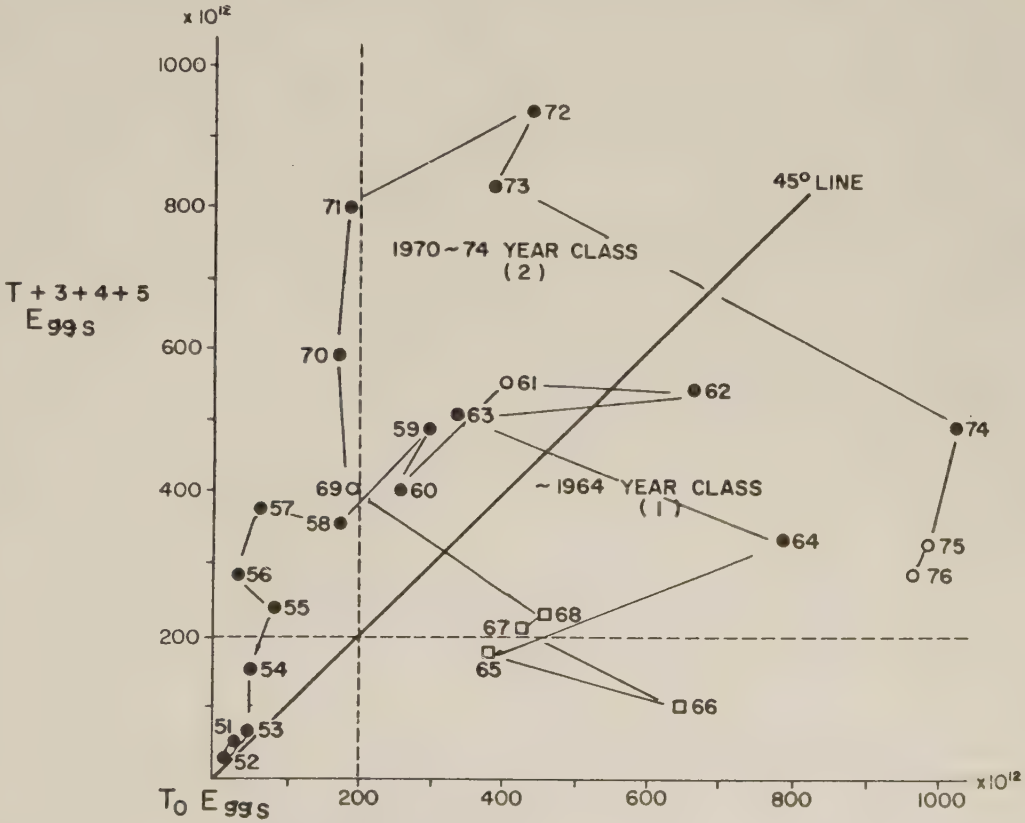


Fig. 8. The data on egg production in any year versus eggs produced by the progeny of those year classes (from Watanabe, this volume) shows a series of complex bloom and recession periods for *Scomber* around Japan. The importance of sequential year class survival and subsequent egg production cannot be ignored, but fitting lines through each time series (i.e. period 1) 1953 to 1964, or 2) 1969 to 1974) does not help one understand or imply any stock-recruitment relation.

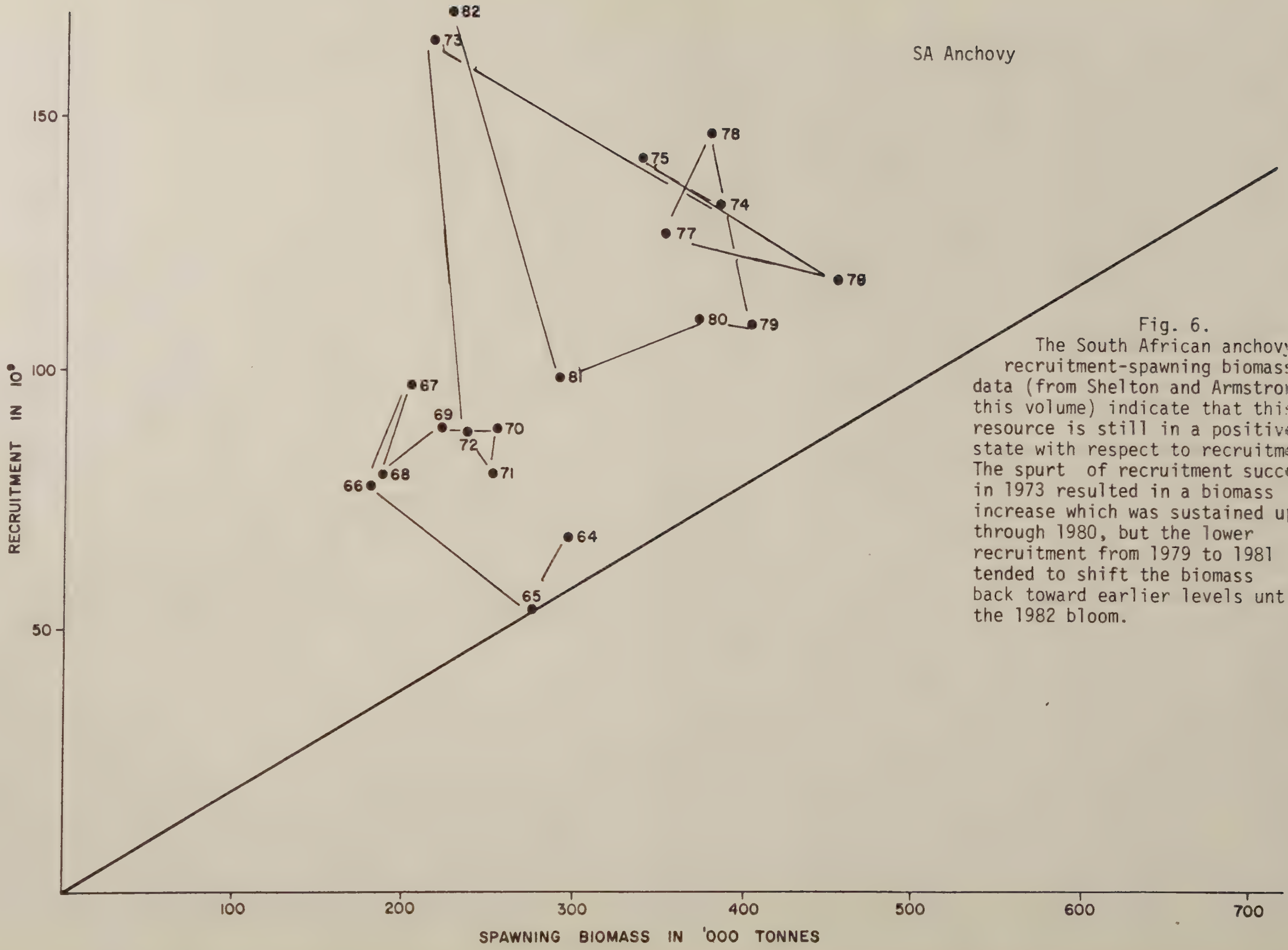


Fig. 6.
The South African anchovy recruitment-spawning biomass data (from Shelton and Armstrong, this volume) indicate that this resource is still in a positive state with respect to recruitment. The spurt of recruitment success in 1973 resulted in a biomass increase which was sustained up through 1980, but the lower recruitment from 1979 to 1981 tended to shift the biomass back toward earlier levels until the 1982 bloom.

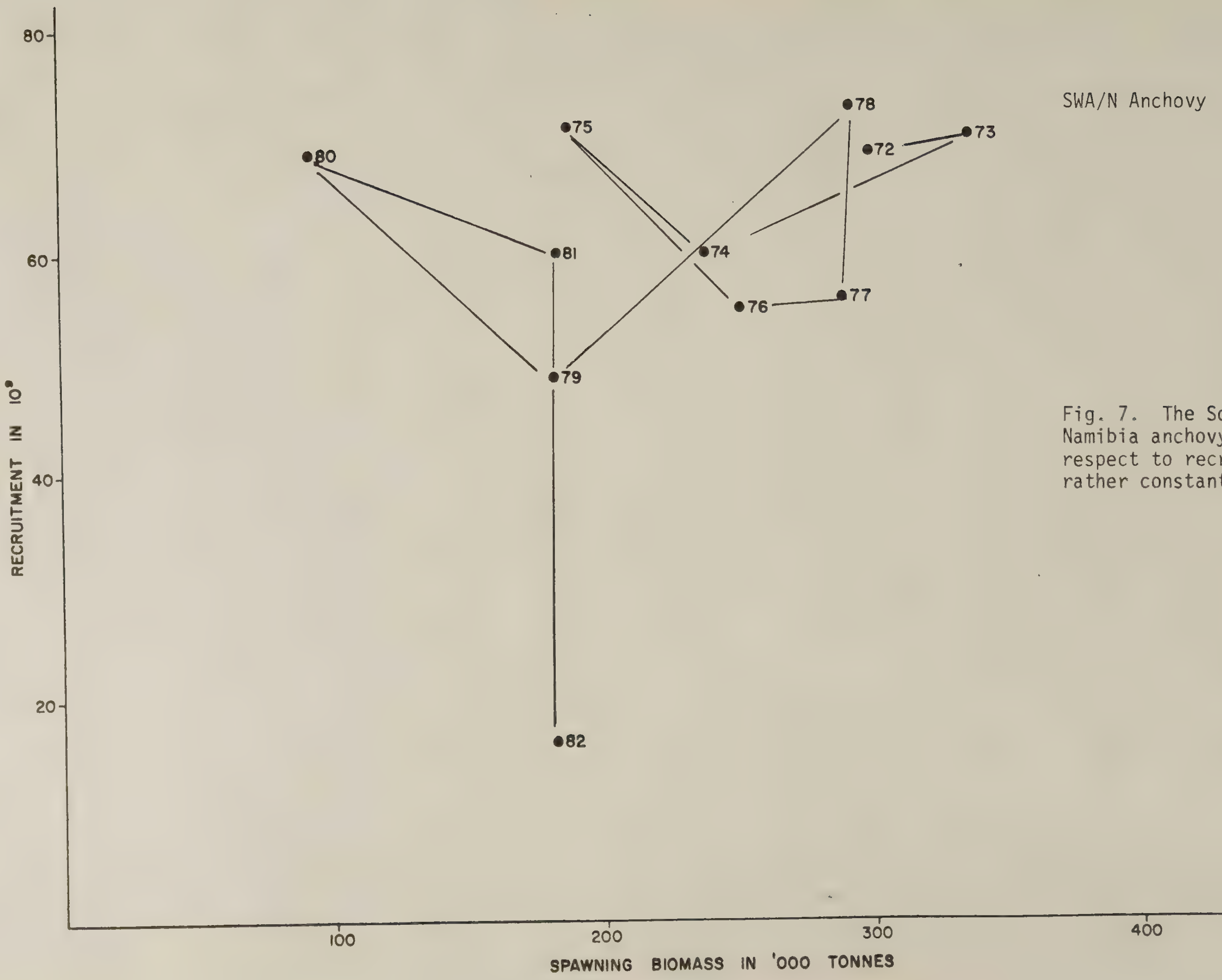


Fig. 7. The Southwest Africa/ Namibia anchovy situation with respect to recruitment appears rather constant up until 1982.

Watanabe (this volume) also presents similar data for the shorter time series, 1960-1978, for *Sardinops melanosticta*. There are two short cycles again indicated with a low period of abundance from 1960 which subsequently declines to unestimably low levels until about 1970, when a new "abundance" cycle began, attaining the heights described in various reports (Tanaka; Hiyashi; and Kawai and Isibasi; all this volume). The egg production cycle began declining again in 1976, and will be an interesting feature to monitor, as suggested by Watanabe (this volume), as an indicator of future stock potential, but not predictive until the recruitment and mature stock abundance is obvious from other measures (Figure 9).

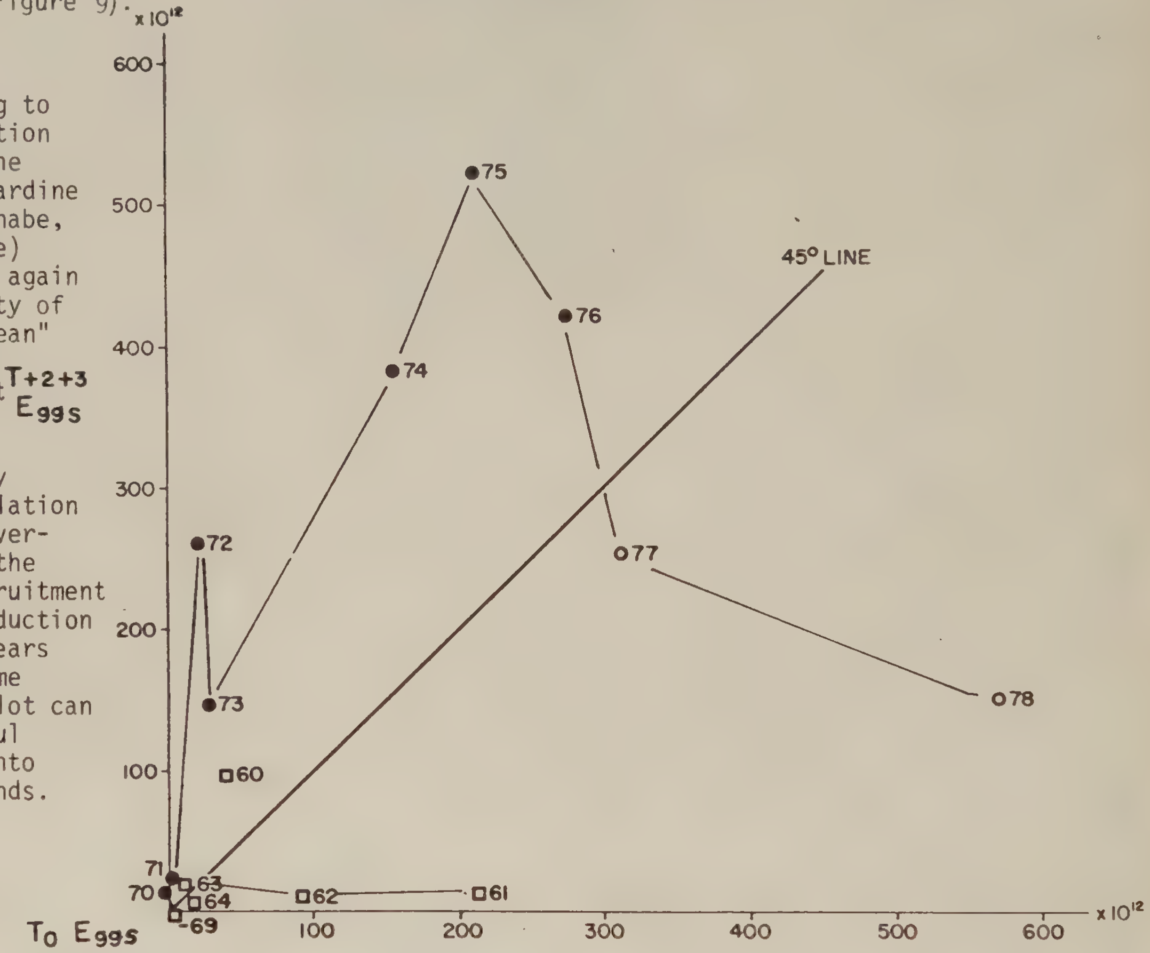


Fig. 9. Similar egg to egg production data for the Japanese sardine (from Watanabe, this volume) shows once again the futility of fitting "mean" stock-recruitment lines to such data. Clearly any implied relation severely over-estimates the likely recruitment or egg production for poor years while a time sequence plot can yield useful insights into likely trends.

The value of this approach is that clear indications of changes in system state are evidenced, lower abundance bounds are made more obvious, and declines are signalled, indicating periods when care should be taken and monitoring of other indicators such as age structure, distribution and abundance blooms of predators should be more closely monitored.

A series of abundance-increase data (which normally compares increased recruitment, increased catches, increased fishing effort, etc.) can easily generate a dome shape curve with a form resembling some presumed stock-recruitment curve, a yield per recruit curve, and even a surplus production curve, all depending on what is the source of the basic data and mostly on what interpretation is being given to it. Fitting a model can therefore be purely artefactual and will normally tend to give the wrong answer to key questions such as: 1) What spawning population abundance will provide for persistent, relatively high potential reproduction? 2) What is the lower level of population which can be expected to support a substantial bloom given the appropriate conditions?

This latter question is posed only by considering these observations and concluding that the bloom cycles are stimulated by non-fishery related phenomena, and are relatively short term. The subsequent increases in distribution and overall abundance, each act to increase potential reproduction, although not necessarily determine their realization. The collapse cycles, on the other hand, do indeed reflect major components of causality in some studies (Csirke 1980; Santander et al., this volume) and warrant further investigation of such features as cannibalism, disease and other density dependent phenomena.

CONCLUSION: WHY MODEL FISHERIES?

In the absence of clear objectives for fishery and fishery related ocean science, there have been significant changes in general attitudes about what these objectives might be. Tautological dialectics about promoting stable fishery production and maintaining species in perpetuity, etc., hardly represent all realistic objectives in the "real-world" of societal demands, growing populations, political economic decisions regarding exploitation and distribution of benefits from renewable marine resources, particularly while facing the perpetual climate-ocean variability which affects each of these.

The main biological variables surveyed here will all need to be considered as potentially strong affectors of fishery models. The simplified models which have evolved have had their utility, and certainly, their severe short comings. The problems of population definitions, basic biological units of interest, and their interactions with other ecosystem components, biotic and abiotic, need to be kept in perspective, and resolved to adequate degrees. Adequate, meaning in this case sufficiently well to be useful in forecasting or predictive models. Hindcasting or historical monitoring models can be (and usually are) less rigorous since they are not critical as bases for immediate decision making.

Even with exploitation unit concepts and resource definitions clearly in hand, modelling has yet to evolve toward a level suggesting the reality of the many changing population responses such as those discussed. Changes in: growth rate; natural mortality rates and sources; carrying capacity at all life stages; distribution and relative abundance; hence density at each stage; all affect the future status of any resource. The changes in age structure, available refugia or determinant processes leading to mortality at any life history stage severely influence any potential to resist either natural or man induced perturbations in the ecosystem.

We are not advocating modelling of the Universe, but only that if any resource is truly important that there be given due consideration to the observations that traditional or conventional fishery models have yet to prove adequate, or even appropriate in many cases. There are obvious exceptions, for example the amazingly stable North Sea plaice, upon which many leading fishery scientists have based their enthusiasm for both age structured and production models. But, ... it should be kept in mind that only diligence by marine ecologists and oceanographers has kept at least one of the major nursery areas (The Wadden Sea) from joining other "industrial wastelands" and thereby insuring, at least temporarily, a future for this component of the production from the North Sea (See Wadden Sea Working Group Reports 1-11, 1982).

Is it likely that specific bivariate plots of each pair of fishery-biological variables will or can hold answers to dynamic fishery questions? Even if the answer is"No"they might and have proved to serve as useful aids in evaluating the appropriateness of many conventional questions. If, no matter how precisely the information gathered, the variables do not give indications of any direct relation, then it is appropriate to declare the question inappropriate, null and void. Reformulation of the question is in order. This is progress. This is what we hoped to achieve during this Consultation.

Other questions needing answers have been discussed here and in other fora (i.e.; Caddy 1983), and two that need particular attention in regard to man's role as major predator are:

1. What are the 'population dynamics' of fishing fleets?
2. What are the determinants of fishery planning on the short and long term, particularly related to econometrics of fishing and dependent, subsequent operations?

If these were well known, it would appear that perhaps managers and decision makers would learn what are appropriate biological questions to ask, and we, as scientists, might be able to formulate and execute research and monitoring schemes to answer them in reasonably synoptic fashion.

Much of marine science can be said to be answering questions for which answers would be nice to know. More important in applied fishery research is that there be more attention paid to formulating answerable questions which need to be known. This is particularly true if we intend to involve other disciplines and fields of interest which have their own immediate problems.

By focussing attention on such phenomena as El Niño, it is possible that there is a misemphasis of important alternative states of the ecosystems involved. Where many are still trying to attribute the demise of the Peruvian anchoveta to the mythical El Niño of 1971-1972, the processes were already well in gear prior to this 'event'. Glantz (1981) has addressed the societal benefits of an El Niño forecast, and inter-governmental bodies have made efforts to not only define El Niño (SCOR Working Group No. 55) but also now scientists have attempted to discover their underlying causes and predict them. Because of the immediacy of the effects draughts and floods, which are among accompanying symptoms of El Niños, are given more attention. However, the fact that El Niño is not regional, but an oceanwide process has only recently been generally recognized. As yet no one has responded at National levels to the consequences of Guillēn's "Anti-El Niño's" on fisheries. Kawasaki (this volume) has provided an interesting correlation between fishery processes across the Pacific Basin which would suggest that modelling and predicting fishery responses has indeed longer term components than only todays fishing effort or todays habitat and ecological status. There is a history and a future which, although they might cycle about some median state, do not permit the broad handed "averaging" of information.

The time to begin facing these problems, reformulating questions and developing new techniques to answer them is now. There is little need for new theory. What is needed is clear headed, pragmatic science of the sort everyone talks about but too few are ready to do, for whatever reasons. The major stumbling blocks to progress usually involve persistent optimism about technological or simple, quick-fix solutions. The solutions lie in hard work at sea, in the laboratory, by innovative multidisciplinary study and gathering of long time series of information, and on a precise knowledge of what are the questions that need answering. The questions needing answers will be posed in a changing societal milieu, and will certainly become more demanding than ever before. If it is recognized that the equilibrium or averaging concepts have proven to hinder rather than help in facing the problem of variations in climate-ocean processes, and their products, fishery potential; and if it is also recognized that the fishery is just one of the many elements to be considered in modelling fisheries, then we may find this to be the age of rediscovery in fishery science.

In the meantime, as fishermen need to fish and resources need to be harvested, sources and patterns of variations should be identified and taken into consideration when interpreting the output of classical models. What is even more important is to evaluate the amount of risk involved by not taking, or not being yet able to take, important externalities into consideration. This will be carefully considered, and any obvious concerns explicitly stated. Until these uncertainties are accounted for it cannot be said that "fishery management" works. It can only be said that there is a lot to be learned before we can be sure we are even approximating adequate monitoring of the complex fishery systems we are charged with sustaining.

ANNEX 1

DISCUSSION OF METHODS OF STOCK CHARACTERIZATION

A1. Protein and enzyme characterizations are possible through a number of techniques which range from electrophoresis and histochemical staining techniques, electrofocussing to chemical purification, and thermodynamic-biochemical function studies. The latter types are extremely costly in time and materials, and are usually only effective at species, or in rare cases at sub-specific levels, for identification of sub-population distinctions. The rare cases would include species isolates with clear distinctions and no mixing.

Protein electrophoresis is the presently dominant technique for rigorous population discrimination procedure in studies of avian and terrestrial vertebrate populations with clearly distinctive barriers to interbreeding, even where some parts of life history stages are coexistent. The applications in the marine environment have been of mixed utility primarily due to misjudgement of the nature of intra-species or sub-population differences.

The statistical requirements and sampling strategies are determined by the non-parametric nature of the data due to the discrete nature of the variation, and the behaviours of the species' populations in reproduction. If a species does not "home" or obviously isolate itself at reproduction, or at some opportune moment for sampling then it is very difficult to obtain sufficient evidence to rigorously define population structures. However, far more inferential power is available in the face of even this problem than is available from category B methods, given the same problems of reproduction behaviour.

A2. Chromosomal comparisons are now classic in species such as *Drosophila* and *Chironomids* which have few, large and highly structured chromosomes. Fishes do not exhibit obvious stratifications from this perspective as their chromosomes are numerous, small, and not yet well described, except for a few species.

The techniques available for studying chromosomal variation are tedious and time consuming, and non-parametric data results, so that these are not promising in studying any but isolated reproductive groups or known spawning fish. Finding no differences cannot, however, be interpreted as being definitive in species with numerous small chromosomes due to the resolution problems described previously.

A3. Mitochondrial DNA is maternally inherited and could be quite useful in studying relations or affinities within and among schools, as hypothesized to exist within similar size fish within schools (Sharp 1978, 1981b). The technique is recent (Giles et al., 1980; Avise et al., 1979; and Lansman et al., 1978) and is useful for relatively limited and intensive studies until better characterized. The absence of a discrete functional quality or character other than size or weight of DNA fragments makes comparisons essentially one of analogy to meristic measures, although heritability is implied. When possible this should be shown rather than assumed. It will be at least a decade before this technique will be evaluated for utility in discriminating breeding units of oceanic species.

A4. Color pattern and pigmentation studies fall into several categories. Where pigmentation is often a developmental (sequential) process, there are often neotenic arrests, or slow downs in individuals within distinct geographic regions. Atlantic albacore exhibit these processes (Aloncle, personal comm.). Whether these are population characteristics or only developmental anomalies due to environmentally induced processes is not likely to be known until culture and laboratory breeding studies of marine fishes is well advanced. On the other hand Perrin (1975) and Evans (1975) have shown that the study of color patterns are useful genetic tools. At present color patterns appear to have limited potential in this area for most fish species.

A5. Immunology has receded from favor in applied studies since the late 1960's because the results of various studies tended to imply far more complexity than was expected in and among species (Deligny, 1969; Sprague, 1967; and Sprague and Fujino, 1965).

The procedures are not difficult and they are both economical and rapid, but the interpretation of results is tedious, often complicated by the effects of ambient conditions where the immune assays are performed, i.e. temperature, light, contaminant aerosols, etc. If a better controlled environment, a special chamber or other mechanisms could be employed to remove these variables, an at-seas sampling programme could be devised to re-evaluate the utility of this tool.

As in electrophoresis, the data are non-parametric, and therefore sample sizes and sampling strategies would need to be rigorous, and these studies are therefore demanding. Breeding studies would be extremely valuable in conjunction with this approach.

A6. Numerical or metrification analyses, as defined here, are multivariate morphometric and/or growth pattern related studies, as opposed to meristic counts. Numerical techniques comprise primarily tedious multivariate data analysis of suspected related groups, contrasted among themselves in order to determine the affinities or levels of relation. Except in clear-cut divergences, close sub-specific groups are likely to be given greater or lesser affinity than closely related but even obviously different species. Numerically derived cladograms can give very opposite results from those based on clearly defined process-related studies of morphology, genetic characters, and even behavioural information (Sharp and Pirages,1978;and Le Gall et al., 1976). However, to find clear, slightly or non-overlapped morphological properties among samples of a species with uniform expectation is a powerful inferential tool even if rarely encountered. The key is in the knowledge of when and where to look. For sub-specific groups which potentially mix, the sampling problems are formidable. For widely distributed species with simultaneous occurrences at extremes of the species habitat, sampling at these points can yield useful and stimulating sampling insights, particularly if studied concomitantly with other category A and B methods.

B1. Growth rate, respiration and developmental sequence are all population specific properties, with great overlap and graded variation within and among populations. In the nomadic species like the tunas, with their great diversity of environmental options, physiological and behavioural responses are also quite diverse; growth rate and onset of maturity studies are still developing, but there are clear dichotomies arising. The studies of Cayré (1981, 1982) on skipjack behaviour and fecundity in the eastern Atlantic indicate at least two different physiological/behavioural groups are frequently encountered where both differences in fecundity at size and school specific fecundity and ovarian state at size are observed.

The importance of population parameters in characterization of resource parameters is fundamental to evaluation of the fishery potentials of the various populations, but such observations as highlighted by Josse et al. (1981), show the great differences and confounding features of studying opportunist species such as tunas in contrast to localized or homing species (Sharp 1981b).

B2. Mark and recapture studies are good for primarily one definitive aspect of "stock" characterization; fish can be shown to move from the point of receiving the mark to the point of recapture. Other inferences will depend heavily upon other data. Since recapture in most fisheries is dependent upon environmental characteristics and the distributions and kinds of fishing effort, unless the entire habitat is fished, the results are often severely biased, hence of limited value to population structure studies.

The application of mark and recapture experiments in defining "stock structure" depends solely upon the supportive data set accompanying the studies. It has not yet been proven for any fish that tagging alone has had a definitive role in determining stock structure, it is solely an inferential aid. Albacore crossing the North Pacific or a codfish crossing the Atlantic does not prove the single genetic stock hypothesis, or panmixis, it only suggests that some population components are actively making transoceanic crossings. Whether there is a single, simple population or several is only proved through characterization studies based on genetic information, principally from A1, 3 and 5.

B3. Natural tags fall into two types, those obtained from the environment which are permanent and those which can be trasnferred and/or lost. Of the first category we have examples of chemical isotopes which arise from point sources in the environment, and incorporated by individuals either directly from solution in the water column, or by dominant food organism concentration, and assimilation, or both. The studies by Calaprice (1971) and Calaprice et al., (1971) have shown useful examples of this type of natural tag in salmonids species arising from known spawning grounds, with characteristic chemical patterns.

Of the second category there are distinctly conflicting possibilities which confound the interpretation of the results, hence diminishing the utility of the tools. Parasite-specific studies fall into this category. If a parasite is carried specifically by a host with a limited geographic range, delimiting the distribution of that parasite, then the parasite is a good marker or natural tag, comparable to those in category B2 for studying the distribution of the host species arising from the parasite's habitat.

However, if the host or the parasite can be separated (lost) or transferred (by predation of the host) by a species with a broader range, then the utility of the parasite as a definitive label, as contrasted to a "distribution" indicator, is lost too. The use of parasites to determine population structure depends heavily upon supporting information and can be corroborative, but is not alone definitive.

Chemical tags have to be evaluated in the same light as parasite information. If for any reason one suspects that the chemical tag can be lost or transferred, then its utility as a delimiting character is lost.

Natural tags in hard parts can act as records of life history processes. Oxygen isotope ratios can yield information on temperature exposure, and the changes of habitat, i.e., fresh to saline, saline to freshwater, can certainly be observed. Fishes with complex life history patterns in local regions could be studied quite usefully in this regard, while mesopelagics and most tunas, with their subsurface, thermocline centered habitats, prove more of a problem both logically and realistically.

The problem reduces to one of observations on Lagrangian water motion and water mass parcel distributions in the ocean. Rossby, of the Woods Hole Institution of Oceanography, has studied for several years the Lagrangian transport of SOFAR floats through acoustic methods across the North Atlantic from the mouth of the Mediterranean to the west across the Atlantic Ocean, throughout the Sargasso and Gulf Stream related water masses. The complexity is astounding. The upper and lower thermocline transport is relatively independent. Studies of chemical tags could be quite misleading.

B4. Meristic counts, like life history patterns and natural tags are due to local, but short-term exposures, with genetic underpinnings. The causal studies of Lindsay (1961) and Taning (1952) show extreme meristic variation. Differences are primarily dependent upon such variables as temperature exposure and development time. These are neither definitive nor inferential data without several concomitant information sets. For example, if one could use oxygen isotope ratios from chemical tag studies of hard-parts to characterize temperature epochs of early life history stages along with meristic counts, perhaps single populations spread over broad geographic ranges (latitudinal or depth) could be interpreted to comply with a simple stock concept. The important initial data would be category A studies. Without those data the meristic sampling observations could be entirely misleading and illogical bases for drawing conclusions on population structure. Gibbs and Collette (1967) show that meristics are barely useful as species identification tools for the genus *Thunnus*.

For opportunistic and widely distributed species it is unlikely that any of these data sets (A or B) will, alone, be adequate. Other sets of data which can be useful are length-age frequency data and sex ratio with size. These permit an evaluation of a few behavioural parameters, as yet not given appropriate attention in population studies.

REFERENCES

Aiken, J. 1981. A chlorophyll sensor for automatic, remote, operation in the marine environment. Mar.Ecol.Prog.Ser. 4:235.

Alheit, J., B. Alegre, V.H. Alarcón and B. Macewicz. (This volume). Batch fecundity and spawning frequency of various anchovy (genus: Engraulis) populations from upwelling areas and their use for spawning biomass estimates.

Alvariño, A. 1980. The relation between the distribution of zooplankton predators and anchovy larvae. Calif.Coop.Oceanic Fish.Invest.Rep. XXI:150-160.

Andersen, K.P. and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd.Dan.Fisk. Havunders. N.S. 7:319-435.

Avise, J.C., R.A. Lansman and R.O. Shade. 1979. The use of restriction endonucleases to measure mtDNA sequence relatedness in natural populations. I. Population structure and evolution in the genus Peromyscus. Genetics. 92:279-295.

Bakun, A. and R.H. Parrish. 1981. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes (G.D. Sharp, ed.). IOC Workshop Report No.28. IOC/UNESCO, Paris.

Bakun, A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean sciences in relation to living resources. Canadian J.Fish.Aquat.Sci. 39(7):1059-1070.

Baranov, T.I. 1918. On the question of the biological basis of fisheries. Nauch.issledov.iktiol, Inst.Izv. 1(1):81-128. Izv.ryb.i nauch.issledov. 1(1). Moscow.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Invest.London. Ser.2 (19):533 p.

Beyer, J.E. 1976. FISH I. Survival of fish larvae - a single server queue approach. Inst.Math.Stat. Oper.Res., Technical University of Denmark, Lyngby. 244 p.

____________. 1980. Feeding success of clupeoid fish larvae and stochastic thinking. DANA. 1:65-91.

Beyer, J.E. and G.C. Laurence. 1981. Aspects of stochasticity in modelling growth and survival of clupeoid fish larvae. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 178:17-23.

Booke, H.E. 1981. The conundrum of the stock concept: are nature and nurture definable in fishery science? Canadian J.Fish.Aquat.Sci. 38(12):1479-1480.

Caddy, J.F. 1983. An alternative to equilibrium theory for management of fisheries. FAO Expert Consultation on the Regulation of Fishing Effort (Fishing Mortality), 17-26 January 1983, Rome. 42 pp. (In press).

Calaprice, J.R. 1971. X-ray spectrometric and multivariate analysis of sockeye salmon (Onchorynchus nerka) from different geographic regions. J.Fish.Res.Board Can. 28:369-377.

Calaprice, J.R., H.M. McSheffrey and L.A. Lapi. 1971. Radio-isotope X-ray fluorescence spectrometry in aquatic biology: a review. J.Fish.Res.Board Can. 28:1583-1594.

Cayré, P. 1981. Maturité sexuelle fécondité et sex ratio du listao (Katsuwonus pelamis) des côtes d'Afrique de l'Ouest (0ºN-20ºNO, étudiés à partire des débarquements thoniers (1977-1979) au port de Dakar. ICCAT, col. vol. of scient. Papers. 15(2), doc. SCRS/80/54:135-149.

____________. 1982. Qu'est-ce qu'un banc de listao (Katsuwonus pelamis)? Quelques réflexions à partir des observations faites lors des campagnes de marquage. ICCAT, col. vol. of scient. papers. 17(2), doc SYMP/81/5:467-470.

Clark, C.W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J.Cons. 36:7-14.

Clark, C.W. and M. Mangel. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. Fish.Bull.U.S. 77(2):317-337.

Coombes, S.H., J.A. Lindley and C.A. Fosh. (This volume). Vertical distribution of larvae of mackerel (Scomber scombrus) and microplankton, with some conclusions on feeding conditions and survey methods.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp.P.-v.Réun.Cons.int.Explor.Mer. (177):307-313.

Csirke, J. and J. Caddy. 1983. Production modeling using mortality estimates. Canadian J.Fish. Aquat.Sci. 40(1):43-51.

Deligny, W. 1969. Serological and biochemical studies on fish populations. Oceanogr.Mar.Biol.Ann. Rev. 7:411-513.

Dessurault, J.G. 1976. 'Batfish': a depth controllable towed body for collecting oceanographic data. Ocean Engin. 3:99-111.

Erwick, L.K., S.D. Flam and T.E. Olsen. 1979. Comprehensive modelling in fisheries. Comments and case study. Paper presented at the NATO Symposium on applied operation research in fishing. Trondheim, Norway, 14-17 August 1978. Preprints vol.2.

Evans, W.E. 1975. Distribution and differentiation of populations, and other aspects of the natural history of Delphinus delphis Linnaeus in the northeastern Pacific. Doctoral dissertation, University of California, Los Angeles. 145 pp.

Fasham, M.J.H. 1978. The statistical and mathematical analysis of plankton patchiness. Oceanogr. Mar.Biol.Ann.Rev. 16:43-79.

Fedra, K. 1980. Mathematical modelling. A management tool for aquatic ecosystems? Helgolander meeresuntersuchungen. 34(2):221-235.

Fontana, A. 1981. Milieu marin et ressources halieutiques de la République Populaire du Congo. Trav.et Doc.de l'ORSTOM. (138):350 p.

Francis, R.C. 1977. TUNPØP, a simulation of the dynamics and structure of the yellowfin tuna stock and surface fishery of the eastern Pacific Ocean. Bull.Inter-Amer.Trop.Tuna Comm. 17(4):215-269.

Garcia, S. 1983. The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations? Oceanogr.Trop. Vol.18, No.1.

Garcia, S. and L. Le Reste. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish.Tech.Pap. (203):215 p.

Garrod, D.J. 1964. Effective effort and the catchability coefficient, q. Rapp.P.-v.Réun.Cons.int. Explor.Mer. 155(2):66-70.

Gibbs, R.H., Jr. and B.B. Collette. 1967. Comparative anatomy and systematics of the tunas, genus Thunnus. Fish and Wildl.Ser.Fish.Bull. 66(1):65-130.

Giles, R.E., H. Blanc, H.M. Cann and D.C. Wallace. 1980. Maternal inheritance of human mtDNA. Proc.Natl.Acad.Sci. 77:6715-6719.

Glantz, M.H. 1981. Considerations of the societal value of an El Niño forecast and the 1972-1973 El Niño. pp. 449-476. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York, Chichester, Brisbane, Toronto.

Glantz, M.H. and J.D. Thompson (eds). 1981. Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries. Advances in Environmental Sciences and Technology. Vol.II. John Wiley and Sons, New York, Chichester, Brisbane, Toronto. 491 p.

Graham, G.M. 1935. Modern theory of exploiting a fishery and its application to North Sea trawling. J.Cons. 10:264-274.

____________. 1939. The sigmoid curve and the overfishing problem. Rapp.P.-v.Réun.Cons.int. Explor.Mer. 110(2):15-20.

Greenblatt, P. 1982. Distribution of volume scattering observed with an 87.5 kHz sonar. J.Acoust. Soc.Am. 71(4):879-885.

Guillén, O. and R. Callienes. 1981. Biological productivity and El Niño. pp. 255-284. In Resource Management and Environmental Uncertainty: lessons from coastal upwelling fisheries. John Wiley and Sons, New York, Chichester, Brisbane, Toronto.

Hanamoto, E. 1975. Fishery oceanography of bigeye tuna. II. Thermocline and dissolved oxygen content in relation to tuna longline fishing grounds in the eastern tropical Pacific Ocean. La Mer (Bull.Soc.Franco-Japonaise d'oceanographie). 13(2):58-71.

Hedgpeth, J.W. 1977. Models and muddles: some philosophical considerations. Helgoland Wiss. Meeresunters. 30(1-4):92-104.

Hennemuth, R.C., J.E. Palmer and B.E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. J.Northw.Atl.Fish.Sci. 1:101-111.

Hewitt, R. 1982. Spatial pattern and survival of anchovy larvae: Implications of adult reproduction strategy. Ph.D. disseration, University of California at San Diego. 187 p.

Hiyashi, S. (This volume). Some explanation for changes in abundances of major neritic-pelagic stocks in the northwest Pacific Ocean.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 20:1-228.

Hunter, J.R. 1980. The feeding behavior and ecology of marine fish larvae. pp. 287-330. In Fish Behavior and its Use in the Capture and Culture of Fishes (J.E. Bardach et al., eds). ICLARM, Manila.

Hunter, J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish.Bull.U.S. 77:641-652.

Hunter, J.R. and B.J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning in the northern anchovy, Engraulis mordax. Fish.Bull.U.S. 78.

IOC Workshop Report No.28. 1981. Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, 20 April-5 May 1980 (G.D. Sharp, ed.). Inter-governmental Oceanographic Commission, Unesco, Paris. 323 p.

Jones, R. 1973. Density dependent regulation of the numbers of cod and haddock. Rapp.P.-v.Réun.int.Explor.Mer. 164:156-173.

Jones, R. and J.R.G. Hislop. 1978. Changes in North Sea haddock and whiting. Rapp.P.-v.Réun. Cons.int.Explor.Mer. 172:58-71.

Josse, E., J.C. Le Guen, R. Kearney, A. Lewis, A. Smith, L. Marec and P.K.Tomlinson. 1979. Growth of skipjack. Occasional paper No.11. South Pacific Commission, Noumea. 83 pp.

Kawai, T. and K. Isibasi. (This volume). Change in the abundance and species composition of neritic pelagic fish stocks in connection with larval mortality caused by cannibalism and predatory loss by carnivorous plankton.

Kawasaki, T. (This volume). Why do some pelagic fishes have wide fluctuations in their numbers? - Biological basis of fluctuation from the viewpoint of evolutionary ecology.

Kishinouye, K. 1923. Contributions to the comparative study of the so-called scombroid fishes. J.Coll.Agric.Imper.Univ.Tokyo. 8(3):293-475.

Kondo, K. 1980. The recovery of the Japanese sardine - the biology basis of stock size fluctuations. Rapp.P.-v.Réun.Const.int.Explor.Mer. 177:332-352.

Lansman, R.E., R.O. Shade, J.F. Shapira and J.C. Avise. 1978. The use of restriction endonucleases to measure mtDNA sequence relatedness in natural populations. III. Techniques and potential application. J.Mol.Evol. 17:214-226.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish.Bull.U.S. 73(3):453-462.

__________. 1978. The relation betwen oceanographic conditions and larval anchovy in the California Current: identification of factors contributing to recruitment failure. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 173:212-230.

Laurec, A. and A. Maucorps. 1981. Note sur l'utilisation des règles de décision en gestion des stocks. CIEM/CM 1981/H:37:18 p. plus figs (Mimeo).

Lebedev, N.V. 1970. Elementary populations of fish. Jerusalem, Israel Program for Scientific Translations, No. 5480.

Le Gall, J.Y., A. Laurec and P. Chardy. 1976. Mise en évidence des relations phénotypiques et phylogénétiques à l'intérieur du genre Thunnus par une analyse multicritère. Bull.Mus.Nat. Hist.Nat.Sci. 3(339):1349-1368.

Lindsay, C.C. 1961. The bearing of experimental meristic studies on racial analyses of fish populations. Proc.Poc.Sci.Congr.Bangkok. 1952:54-58.

Longhurst, A.R. and R. Williams. 1976. Improved filtration systems for multiple-serial plankton samplers and their deployment. Deep-Sea Res. 23:1067.

Lord, G.E. 1976. Decision theory applied to the simulated data acquisiton and management of a salmon fishery. Fish.Bull.U.S. 74(4):837-845.

MacCall, A.D. 1981. The consequences of cannibalism in the stock-recruitment relationship. pp. 201-220. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes (G.D. Sharp, ed.). Workshop Report No.28. IOC/UNESCO, Paris.

Mackas, D. and C. Boyd. 1979. Spectral analysis of zooplankton spatial heterogeneity. Science. 204:62-64.

Nakamura, H. 1969. Tuna distribution and migration. Fishing News (Books) Ltd., London. 76 pp.

O'Connell, C.P. 1980. Percentage of starving northern anchovy, Engraulis mordax, larvae in the sea, as estimated by histological methods. Fish.Bull.U.S. 78:475-489.

Owen, R.W. 1981. Patterning of flow and organisms in the larval anchovy environment. pp. 167-200. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. (G.D. Sharp, ed.). Workshop Report No.28. IOC/UNESCO, Paris.

Paloheimo, J.E. and L.M. Dickie. 1964. Abundance and fishing success. Rapp.P.-v.Réun.Cons.int. Explor.Mer. 155(2):152-164.

Paloheimo, J.E. and R.C. Plowright. 1979. Bioenergetics, population growth and fisheries management. pp. 262-268. In Environmental Biomonitoring, Assessment, Prediction and Management (J. Cairns, G.P. Patil and W.E. Waters, eds). Int.Coop.Publ.House, Fairland, Maryland, USA. 262-268.

Parrish, R.H. and D.L. Mallicoate. (This volume). Analysis of fishery data from the California anchovy fishery. The role of adult processes in population fluctuations.

Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. (This volume). Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction.

Pauly, D. 1979. Theory and management of tropical multispecies stocks: A review, with emphasis on the Southeast Asian demersal fisheries. International Center for Living Aquatic Resources Management, Manila. ICLARM Stud.Rev. 1:35 p.

Pauly, D. and I. Tsukayama. (This volume). On the seasonal growth, monthly recruitment and monthly biomass of Peruvian anchoveta (Engraulis ringens) from 1961 to 1979.

Perrin, W.F. 1975. Variation of spotted and spinner porpoise (Genus Stenella) in the eastern Pacific and Hawaii. Bull.Scripps.Inst.Ocean. 21:206 pp.

Pingree, R.D., P.M. Holligan and G.T. Mardell. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European continental shelf. Deep-Sea Res. 25:1011-1028.

Platt, T. and K. Denman. 1975. Spectral anlysis in ecology. Ann.Rev.Ecol.Syst. 6:189.

Pope, J.G. 1980. Some consequences for fisheries management of aspects of the behaviour of pelagic fish. Rapp.P.-v.Réun.Cons.int.Explor.Mer. 177:466-476.

Pope, J.G. and D.J. Garrod. 1975. Sources of error in catch and effort quota regulations with particular reference to variations in the catchability coefficient. Res.Bull.Int.Comm.NW.Atl. Fish. 11:17-30.

Richardson, B.J. (In press). The distribution of protein variation in skipjack tuna (Katsuwonus pelamis) from the central and south western Pacific. Aust.J.Mar.Freshw.Res.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish.Res.Board Can. 119:300 pp.

Rosenthal, H. 1970. Anfutterung und Wachstum der Larven und Jungfische des Hornhechts Belone belone. Helgolaender Wiss.Meeresuntersuch. 21:320-332.

Russell, J.S. 1931. Some theoretical considerations on the "overfishing problem". J.Cons.Explor.Mer. 6:3-27.

Saito, S. 1973. Studies on fishing of albacore, Thunnus alalunga (Bonnaterre) by experimental deepsea tuna long-line. Mem.Fac.Fish.Hokkaido Univ. 21(2):184 pp.

____________. 1975. On the depth capture of bigeye tuna by further improved vertical long-line in the tropical Pacific. Bull.Jap.Soc.Sci.Fish. 41(8):831-841.

Sameoto, D.D. 1981. Horizontal and vertical distributions of zooplankton numbers and biomass off the coast of Peru. Bol.IMARPE, Vol.extraordinario. 164-170.

Sameoto, D.D., L.O. Jaroszinski and W.B. Fraser. 1980. The BIONESS, a new design in multiple net zooplankton samplers. Canadian J.Fish.Aquat.Sci. 37:722.

Santander, H., J. Alheit, A.D. MacCall and A. Alamo. (This volume). Egg mortality of the Peruvian anchovy (Engraulis ringens) caused by cannibalism and predation by sardines (Sardinops sagax).

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull.Int.Am.Trop.Tuna Comm. 1(2):26-56.

Sharp, G.D. 1976. Vulnerability of tunas as a function of environmental profiles. In Maguro Gyogo Kyogikay Gijiroku, Suisancho - Enyo Suisan Kenkyusho (Proceedings of Tuna Fishery Research Conference, Fisheries Agency, Far Seas Fisheries Research Laboratory, Japan). In English and Japanese.

___________. 1978. Behavioral and physiological properties of tuna and their effects on vulnerability to fishing gear. pp. 397-450. In The Physiological Ecology of Tunas (G.D. Sharp and A.E. Dizon, eds). Academic Press, New York, San Francisco, London.

___________. 1979. Areas of potentially successful exploitation of tunas in the Indian Ocean with emphasis on surface methods. IOFC/DEV/79/47. 55 pp.

___________ (ed.). 1981a. Intergovernmental Oceanographic Commission Workshop Report No.28. Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes. 20 April - 5 May 1980. Lima, Peru. IOC/UNESCO, Paris. 323 p.

___________. 1981b. Colonization: modes of opportunism in the ocean. pp. 125-148. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, 20 April - 5 May 1980, Lima, Peru. IOC Workshop Report Series No.28. IOC/UNESCO, Paris.

___________. 1983. (In press). Ecological efficiency and activity metabolism. In Flows of Energy and Materials in Marine Ecosystems (M.J.L. Fasham, ed.). NATO Advanced Research Institute, Bombanne, France, 12-20 May 1982. Plenum Press.

Sharp, G.D. and A.E. Dizon (eds). 1978. The physiological ecology of tunas. Academic Press, New York, San Francisco and London. 506 pp.

Sharp, G.D. and S.W. Pirages. 1978. The distribution of red and white swimming muscles, their biochemistry and the biochemical phylogeny of selected scombroid fishes. pp. 41-78. In The Physiological Ecology of Tunas (G.D. Sharp and A.E. Dizon, eds). Academic Press, New York.

Shelton, P.A. and M.J. Armstrong. (This volume). Variations in the parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system.

Skud, B.E. 1982. Dominance in fishes: the relation between environment and abundance. Science. 216:144-149.

___________. (This volume). Interactions of pelagic fishes and the relation between environmental sections and abundance.

Smith, P.E., H. Santander and J. Alheit. (This volume). Comparison of egg sample probability distributions of the anchovy (Engraulis ringens) and sardine (Sardinops sagax) off Peru and the anchovy (E. mordax) and the sardine (Sardinops caerulea) off California.

Smith, S.L., C.M. Boyd and P.V.Z. Lane. 1981. Short-term variation in the vertical distribution of copepods off the coast of northern Peru as determined by particle counting. (ICAEN) IMARPE, Bol. Vol.extraordinario:103-111.

Sprague, L.M. 1967. Multiple molecular forms of serum esterase in three tuna species from the Pacific Ocean. Hereditas. 57:198-205.

Sprague, L.M. and K. Fujino. 1965. Serum polymorphisms of the skipjack (Katsuwonus pelamis) and the yellowfin (Neothunnus macropterus) tunas. Genetics. 52:467-477.

Sund, P.N., M. Blackburn and F. Williams. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr.Mar.Biol.Ann.Rev. 19:443-512.

Suzuki, Z. and S. Kume. 1982. Fishing efficiency of deep longline for bigeye tuna in the Atlantic as inferred from the operations in the Pacific and Indian Oceans. ICCAT Col.Vol.Sci.Pap. XVII:471-486.

Tanaka, S. (This volume). Variation of pelagic fish stocks in waters around Japan.

Taning, A.V. 1952. Experimental study of meristic characters in fishes. Biol.Rev.Cambridge Philos. Soc.

Theilacker, G. and K.T. Dorsey. 1981. Larval fish diversity, a summary of laboratory and field research. pp. 105-142. In Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes (G.D. Sharp, ed.). Workshop Report No.28. IOC/UNESCO, Paris.

Uda, M. 1927. Relation between the daily catch statistical studies in the influence of cyclone upon the fishing. J.Imper.Fish.Inst. 23(3):80-88.

____________. 1952. On the relation between the variation of the important fisheries conditions and the oceanographical conditions in the adjacent waters of Japan. J.Tokyo Univ.Fish. 38(3):363-369.

Ursin, E. 1982. Stability and variability in the marine ecosystem. DANA. 2:51-67.

Vlymen, W.J. 1974. Swimming energetics of the larval anchovy, Engraulis mordax. Fish.Bull.U.S. 72:885-899.

____________. 1977. A mathematical model of the relationship between larval anchovy (E. mordax) growth, prey microdistribution and larval behaviour. Environ.Biol.Fishes. 2:211-233.

Watanabe, T. (This volume). Stock assessment of common mackerel and Japanese sardine along the Pacific coast of Japan by spawning survey.

Zijlstra, J.J., R. Dapper and J.W. Witte. 1982. Settlement, growth and mortaltiy of post-larval plaice (Pleuronectes platessa) in the eastern Wadden Sea. Neth.J.Sea Rev. 15(2).

Zuta, S., I. Tsukayama and R. Villanueva. (This volume). El ambiente marino y los fluctuaciones de los principales poblaciones pelagicos de la costa peruana.

M-43
ISBN 92-5-001447-3